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Published at the Museum of Zoology, The University of Michigan, Ann Arbor, Michigan 48109, U.S.A., by the Society for Experimental and Descriptive Malacology.

ON THE COVER — Shells of the family Viviparidae. Illustrations by John L. Tottenham.

1979

MALACOLOGICAL REVIEW

ANN ARBOR, MI
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12 (1-2)

1979

MALACOLOGICAL REVIEW

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MALACOLOGICAL REVIEW

VOLUME 12, Number 1-2 1979

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COMPARATIVE SPERMATOZOON MORPHOLOGY AND BIVALVE PHYLOGENY

J. David Popham[1]

ABSTRACT

An attempt was made to determine whether or not the fine structure of the spermatozoa of bivalves could be correlated with the currently interpreted evolutionary history of this group. The present results show that only some marine-dwelling species have spermatozoa with an axial rod associated with the acrosome. This feature is found in 2 subclasses of the bivalves sampled. Evidence is presented suggesting that the size of the osmiophilic granule of the acrosome may be correlated with either brooding behavior of some bivalves (brooders having a tendency to have smaller acrosomes than non-brooders); or with the thickness of the egg jelly coats (species having thick egg coats tend to have sperm with large acrosomes). A sperm having its acrosome associated with the middle piece is also described. Neither the sperm nucleus nor mitochondria seemed to show subclass specific characteristics or features associated with different modes of fertilization in the bivalves. On the other hand, features of the acrosome, i.e., whether or not it had an axial rod, or whether or not it was attached to the nucleus, provided evidence to tentatively conclude that sperm structure in bivalves may be correlated with the evolution of species within that group.

INTRODUCTION

Variations in the morphology of spermatozoa appear to be well correlated with the evolution of a number of animal groups such as insects (Baccetti, 1970), crustaceans (Brown, 1970), reptiles (Furieri, 1970), flatworms (Hendelberg, 1970) and echinoderms (Chia et al., 1975); and have been distinctive enough to help resolve controversies over, and to confirm conclusions about, the phylogenetic relationships between groups within the Marsupia (Hughes, 1965) and Gastropoda (Franzen, 1955). Reports such as those just cited, plus acceptance of the concept that the morphology of the spermatozoa appears to be conservative (Tuzet, 1950; Brown, 1970; Chia et al., 1975), a feature necessary for assessing phylogenetic relationships (Douvillé, 1912, 1913), lead us to support the contention that the structure of the spermatozoon in the bivalves might be related to the systematics of this group (Gharagozlou-van Ginneken & Pochon-Masson, 1971; Daniels et al., 1971; Popham et al., 1974). Since comparative studies on the morphology of the soft parts of many extant bivalves may complement those on the fossil record of the hard parts (Newell, 1969a), the fine structure of the spermatozoa of specimens of 5 bivalve species was studied to see if the resulting data conformed to the accepted theories (cf. Cox, 1960; Morton, 1963; Stasek, 1963; Newell, 1965, 1969a) of the evolution of the Bivalvia.

The sperm of the bivalves generally has a primitive or basic form (Retzius, 1905; Franzen, 1956, 1970). That is to say, the sperm usually consists of an ellipsoid or conical nucleus, an acrosome of variable complexity, a middle piece consisting of an aggregation of usually 4-5 mitochondria surrounding a pair of centrioles, and a flagellum or sperm tail (Retzius, 1905; Franzen, 1970). The fine structure of these constituents of the bivalve sperm have been

[1] Present address: Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia, Canada V5A 1S6.

TABLE 1. Summary of higher classification and features of sperm of bivalves in which the fine structure of the sperm has been investigated.

Species	Higher Classification		Features of Sperm
Nucula hartvigiana (Popham & Marshall, 1977)	subclass	Paleotaxodonta	nucleus: long, conical
	order	Nuculoida	acrosome: no axial rod
	superfamily	Nuculacea	middle piece: 4 mitochondria
	family	Nuculidae	
Anadara trapezia (this paper)	subclass	Pteriomorphia	nucleus: ovoid
	order	Arcoida	acrosome: no axial rod
	superfamily	Arcacea	middle piece: 4 mitochondria
	family	Arcidae	
	subfamily	Anadarinae	
Mytilus edulis *Mytilus perna* (Niijima & Dan, 1965) (Bourcart et al., 1965)	subclass	Pteriomorphia	nucleus: ovoid
	order	Mytiloida	acrosome: large granule, axial deeply inserted into nucleus
	superfamily	Mytilacea	
	family	Mytilidae	
	subfamily	Mytilinae	middle piece: 5 mitochondria
Crassostrea virginica (Galtsoff & Philpot, 1960) (Daniels et al., 1971)	subclass	Pteriomorphia	nucleus: ovoid
	order	Pterioida	acrosome: axial rod deeply inserted into nucleus
	superfamily	Ostreacea	
	family	Ostreidae	middle piece: 4 mitochondria
	subfamily	Ostreinae	
Anomia descripta (this paper)	subclass	Pteriomorphia	nucleus: ovoid
	order	Pterioida	acrosome: no axial rod
	suborder	Pterina	middle piece: 4 mitochondria
	superfamily	Anomeacea	
	family	Anomiidae	
Hyriopsis schlegelii (Higashi, 1964)	subclass	Paleoheterodonta	nucleus: cylindrical
	order	Unionoida	acrosome: minute or non-existent
	superfamily	Unionacea	
	family	Unionidae	middle piece: 4 mitochondria
	subfamily	Unioninae	
Ligumia subrostrata (Trimble & Gaudin, 1975)	subclass	Paleoheterodonta	nucleus: cylindrical
	order	Unionoida	acrosome: minute or non-existent
	superfamily	Unionacea	
	family	Unionidae	middle piece: 4 mitochondria
	subfamily	Lampsilinae	
Turtonia minuta (Ockelmann, 1964) This is a light microscope work, but it is relevant because the species is a brooder of its young.	subclass	Heterodonta	nucleus: very long
	order	Veneroida	acrosome: not detailed
	superfamily	Cyamiacea	middle piece: 4 mitochondria
	family	Turtoniidae	

TABLE 1. (Cont.)

Species	Higher Classification		Features of Sperm
Spisula solidissima (Longo & Anderson, 1969)	subclass	Heterodonta	nucleus: ovoid
	order	Veneroida	acrosome: axial rod only partially inserted into nucleus
	superfamily	Mactracea	
	family	Mactridae	middle piece:
Corbicula sandai (Hachiri & Higashi, 1970)	subclass	Heterodonta	nucleus: cylindrical
	order	Veneroida	acrosome: separated from nucleus
	superfamily	Corbiculacea	
	family	Corbiculidae	middle piece: 4 cylindrical mitochondria
Tapes (Ruditapes) decussatus (Pochon-Masson & Gharagozlou, 1970)	subclass	Heterodonta	nucleus: very long, conical
	order	Veneroida	acrosome: long, axial rod only partially inserted into nucleus
	superfamily	Veneracea	
	family	Veneridae	middle piece: 4 spherical mitochondria
Fulvia tennuicostata (this paper)	subclass	Heterodonta	nucleus: ovoid
	order	Veneroida	acrosome: no axial rod
	superfamily	Cardiacea	middle piece: 4 mitochondria
	family	Cardiidae	
	subfamily	Laevicardeinae	
Notocorbula vicaria (this paper)	subclass	Heterodonta	nucleus: ovoid
	order	Myoida	acrosome: no axial rod
	superfamily	Myacea	middle piece: 4 mitochondria
	family	Corbulidae	
	subfamily	Corbulinae	
Barnea candida (Pasteels & Harven, 1962)	subclass	Heterodonta	nucleus: cylindrical
	order	Myoida	acrosome: reticulated, axial rod not inserted into nucleus
	superfamily	Pholadarea	
	family	Pholadidae	middle piece: 4 mitochondria
Bankia spp. (Popham et al., 1974) (Popham, 1974a)	subclass	Heterodonta	nucleus: cylindrical (inflated)
	order	Myoida	acrosome: relatively large, axial rod only partially inserted in nucleus
	superfamily	Pholadacea	
	family	Teredinidae	
	subfamily	Bankiinae	middle piece: 4 mitochondria

TABLE 1. (Cont.)

Species	Higher Classification		Features of Sperm
Lyrodus spp. *Teredo spp.* (Popham, 1974a)	family subfamily	Teredinidae Teredininae	nucleus: cylindrical or conical acrosome: relatively small, axial rod not inserted into nucleus middle piece: 4 mitochondria
Myodora brevis (this paper)	subclass order superfamily family	Anamalodesmata Pholadomyoidea Pandoracea Myochamidae	nucleus: cylindrical acrosome: no axial rod, near middle piece middle piece: 4 mitochondria

described in approximately 14 genera representing 3 of the 7 subclasses (following Newell's classification of 1965, 1969a). The major divisions of the classification of these species are listed in Table 1 along with a brief listing of the important features of the sperm.

The least variable structures appear to be the tail, centrioles and mitochondria. The mitochondria have been found to be intimately associated with the nuclear envelope, spherical to ovoid in shape and 4-5 in number in *Crassostrea virginica*[2] (Galtsoff & Philpott, 1960; Daniels et al., 1971), *Barnea candida* (Pasteels & Harven, 1962), *Hyriopsis schlegelii* (Higashi, 1964), *Mytilus perna* (Bourcart et al., 1965), *Mytilus edulis* (Longo & Dornfield, 1967), *Spisula solidissima* (Longo & Anderson, 1969), *Corbicula sandai* (Hachiri & Higashi, 1970), 4 venerids (Pochon-Masson & Gharagozlou, 1970; Gharagozlou-van Ginneken & Pochon-Masson, 1971) and 6 teredines (Popham, 1974a; Popham et al., 1974), *Ligumia subrostrata* (Trimble & Gaudin, 1975) and *Nucula hartvigiana* (Popham & Marshall, 1977). Sperm having such mitochondria have been described by André (1962) as representing Type II sperm or those sperm in which the mitochondria are little differentiated from those found in somatic cells. Favard & André (1970) have concluded that the morphology of mitochondria in sperm is not useful in determining evolutionary tendencies, at least when considered in relation to viewing the animal kingdom as a whole, but reflects whether or not the sperm is from an external or internal fertilizing species. They thus agree with similar conclusions previously reached by Franzen (1955, 1956, 1970).

The nucleus shows greater morphological diversity than the mitochondria since it can be ovoid (*Mytilus* spp.; cf. Niijima & Dan, 1965; Bourcart et al., 1965), short and conical (*Lyrodus pedicellatus*; Popham, 1974a), nearly spherical (*Crassostrea virginica*; Galtsoff & Philpott, 1960; Daniels et al., 1971), barrel-shaped (*Spisula solidissima*; Longo & Anderson, 1969), pencil-shaped (*Corbicula sandai*; Hachiri & Higashi, 1970) or long, tapering and curved (*Tapes (Ruditapes) decussatus*; Pochon-Masson & Gharagozlou, 1970). Fawcett et al. (1971) and Rattner (1972) have shown that the shape of the nucleus in mammalian sperm is probably dependent upon how the chromatin becomes condensed. Variations in the pattern of nuclear condensation during spermiogenesis has been reported in *M. edulis* (Longo & Dornfield, 1967), *S. solidissima* (Longo & Anderson, 1969) and *T. decussatus* (Pochon-Masson & Gharagozlou, 1970), but whether the final shape of the nucleus of bivalve sperm can be correlated with patterns of chromatin condensation has not been presently reported.

[2] This list refers only to those species for which the author presently knows that the fine structure of the sperm has been described. The valuable light microscope work of Retzius (1905) and Franzen (1955) should still be consulted for a more complete understanding of the structure of bivalve sperm.

In 1956, Franzen suggested that, to a certain extent, the structure of the nucleus may be useful as a systematic character, but later (1970) pointed out that it may also reflect whether or not the sperm is from a species which broods its young. In the later paper, he referred to Ockelmann's (1964) observations that the ovoviviparous *Turtonia minuta* has sperm with not only a large axial ratio but also a helical appearance. The sperm of *Mysella* sp. (*C.* 98736)[3], another neotonous brooder, also has a long axial ratio (Popham, unpubl.).

The acrosome shows extensive morphological diversity in the bivalve sperm and hence may be the most useful structure in assessing phylogenetic relations (Franzen, 1956: 465). However, as pointed out by Baccetti (1970), the evolution of the acrosome should be considered in relation to the evolution of the egg rather than just in relation to the systematics of the fauna being investigated. As previously noted by Franzen (1956), features within the acrosome of the primitive sperm may have arisen independently in unrelated groups and thus have no systematic importance. In other words, the structure of the acrosome may reflect functional adaptions to similar biologies of reproduction (i.e., the brooding phenomenon in such phyletically diverse species as unionids, oysters and teredos) rather than reflect a result of chance mutation which arose in a common ancestor of 2 now phyletically divergent subgroups each maintaining it.

The acrosome of the sperm of most bivalves usually consists of an invaginated vesicle partly covered with or surrounded by periacrosomal material (Dan, 1967). The acrosome vesicle, derived from the Golgi apparatus (Longo & Anderson, 1969; Longo & Dornfield, 1967; Pochon-Masson & Gharagozlou, 1970), can range in complexity by consisting of a very small, poorly developed vesicle as in *Ligumia subrostrata* (Trimble & Gaudin, 1975) at one extreme or by consisting of numerous substances characteristically disposed within it as in *Mytilus edulis* (Niijima & Dan, 1965) at the other; or it can range somewhere between as in *Barnea candida* (Pasteels & Harven, 1962), *Crassostrea virginica* (Galtsoff & Philpott, 1960; Daniels et al., 1971) and *Spisula solidissima* (Longo & Anderson, 1969).

The periacrosomal material may partly consist of an axial rod, a structure usually found occupying much of the volume of the lumen created by the invagination of the acrosomal vesicle. In some species, there is no axial rod, as in *Ligumia subrostrata* (Trimble & Gaudin, 1975). In those species having an axial rod it may be long and penetrate deeply into an anterior nuclear fossa, as in *Mytilus* spp. (Bourcart et al., 1965; Niijima & Dan, 1965) and *Crassostrea virginica* (Galtsoff & Philpott, 1960; Daniels et al., 1971), whereas in others it may be long, but not be inserted and instead extend well forward, as in *Tapes decussatus* (Pochon-Masson & Gharagozlou, 1970) and *Corbicula sandai* (Hachiri & Higashi, 1970); and finally in still others it may be relatively short and remain enclosed only within the lumen created by the invagination of the vesicle, as in *Barnea candida* (Pasteels & Harven, 1962), *Spisula solidissima* (Longo & Anderson, 1969) and the teredos (Popham, 1974a; Popham et al., 1974). It is possible that in those sperm having an axial rod it may play a role in the fertilization of the bivalve oocyte (Niijima & Dan, 1965; Popham, 1974b).

As previously mentioned, some of the differences in the morphology of spermatozoa of the bivalves may be attributed to behavioural adaptations to fertilization of the oocytes. Generally speaking, sperm transmission in the bivalves is such that the sperm are freely discharged into the water, the primitive mode of fertilization (Franzen, 1955, 1970). But in some species, the oocytes are fertilized within the confines of the organism where the developing young are brooded (i.e., the demibranchs of the unionids (Weir, 1969) and the mantle cavity of some teredines (Turner, 1966)). The mode of fertilization is still external because the sperm are not transferred via spermatophores or copulatory organs to the inside of the female reproductive tract (Franzen, 1970). For example, fertilization of the oocytes in the mantle cavity of *Bankia setacea* occurs by the male inserting its excurrent siphon into

[3] Collection number of the Australian Museum, as reported in section on Materials and Methods.

the incurrent siphon of the female and releasing the sperm (Townsley et al., 1965). Adaptations such as the one just described should be included in references to the mode of fertilization in bivalves since the structure of the sperm may be influenced by it. The reason for suggesting this is that Popham (1974a) showed that the spermatozoa of brooding teredines have smaller axial rods and smaller acrosomal vesicles than do non-brooding teredines, even though the structure of these constituents of the sperm were otherwise very similar in the 2 groups. Because of this finding, it is proposed that the morphology of the sperm of *Ligumia subrostrata* and other unionoids may warrant an interpretation other than that given by Trimble & Gaudin (1975). These workers stated that the morphology of sperm resembled that of a typical "broadcast fertilizer". But *L. subrostrata* is a unionid and broods its young (Weir, 1969), and therefore is not a "broadcast fertilizer" *sensu* Franzen (1955: 446). Since other unionid spermatozoa also may have very small acrosomes (Franzen, 1955; Higashi, 1964), the possibility exists that within the unionoids the small acrosome in the sperm may be correlated with the brooding behaviour of females. For instance, it may be that eggs of brooding species (which therefore are protected from the rigours of the external environment) have thinner jelly coats than those of non-brooding species. These conflicting interpretations may possibly be resolved by examining the broadcasted sperm of species within the closely related order Trigonioida or by examining fine structure of the oocytes. It may be noted in passing that Franzen (1955: 445) considered that the sperm of unionids occupied an exceptional position in regard to metazoan sperm in general because they did not show a changed morphology in response to the altered biology of fertilization. In contrast, Trimble & Gaudin's (1975) results appear to demonstrate that the sperm has changed in response to a changed biology of fertilization. However, we do not appear to know at present to what extent an alteration in the biology of fertilization is necessary to induce a corresponding change in the morphology of the sperm.

In conclusion, the present data on the fine structure of spermatozoa of the bivalves may be related to both evolutionary tendencies within a group (Gharagozlou-van Ginneken & Pochon-Masson, 1971) and to behavioural adaptations to fertilization (Popham, 1974a). Both concepts may be valid, with different selection pressures acting on the sperm independently. Obviously sperm of more species should be examined before sufficient information is available to draw lasting conclusions. The purpose of this paper is to partly fill the gap in the knowledge of bivalve sperm structure by reporting the results of a study in which the spermatozoa of 5 bivalve species were examined. Two of the examined species are ascribed to the subclass Pteriomorphia, 2 to the subclass Heterodonta and 1 to the subclass Anamalodesmata, a group in which the sperm has not previously been observed with the electron microscope.

MATERIALS[4] AND METHODS

Specimens of *Anadara trapezia* Deshayes 1839 and *Anomia descripta* Iredale 1936 were collected from the intertidal zone at Rocky Point, Botany Bay (Long. 151° 8' E, Lat. 34° 0' S). Voucher specimens of the species have been deposited in the Australian Museum and have been assigned the collection numbers C. 99342 and C. 98734, respectively. Specimens of *Fulvia tennuicostata* Lamarck 1819, *Notocorbula vicaria* Iredale 1930 and *Myodora brevis* Sowerby 1929 were collected by dredge at approximately 15 m depth in Port Jackson Harbour (Long. 151° 14' E, Lat. 33° 51' S). Voucher

[4] The author gratefully acknowledges the help of Dr. W. Ponder and his staff of the Australian Museum in identifying the specimens, and to Associate Professor C. Phipps of the Department of Geology, University of Sydney, for help in collecting them.

specimens of these species also have been deposited in the Australian Museum and have been assigned the collection numbers C. 98833, C. 99325 and C. 98834, respectively.

The testes were fixed in the same way for all specimens. After the valves were pried apart, the testes were removed, placed in fixative and sliced into small blocks. The fixative consisted of 2½% glutaraldehyde, 0.1 M sodium cacodylate buffer, 2% NaCl, and HCl to adjust the pH of the solution to 7.4. The blocks of testes were post-osmicated in 2% OsO_4 for 2 hours and stained en bloc with 2% uranyl acetate in 50% ethanol. The blocks were dehydrated in ascending concentrations of ethanol, immersed in dry acetone and embedded in Araldite or Spurr's epoxy resin. Ultrathin sections showing silver/gold interference colours were cut from the embedded blocks and mounted on collodin/carbon-coated 200 mesh copper grids and stained with lead citrate (Venable & Coggeshall, 1965).

The length of the spermatozoa was the distance measured between the anterior-most portion of the acrosome and posterior portion of the middle piece of the sperm.

The relative volumes of the osmiophilic acrosomal granule and nucleus of the spermatozoa were determined in a manner previously described in detail by Popham (1974a). The profiles of the osmiophilic granule and nucleus of a median section of a sperm seen in an electron micrograph were cut out and weighed. The relative weights of the structures were proportional to their relative volumes. For the sake of convenience in expression this ratio was termed the profile ratio (see Table 2).

TABLE 2. The weight of a median profile of the osmiophilic substance of the acrosome divided by the weight of the median profile of the nucleus. Numbers in parentheses represent the sample size.

Species	Profile Ratio	Source	Comment
Bankia spp.	0.285-0.312(3)	Popham, 1974a	broadcast fertilizers
Lyrodus spp.	0.059-0.068(3)	Popham, 1974a	brooders
Crassostrea virginica	0.224	Galtsoff & Philpott, 1960	broadcast fertilizers
Mytilus edulis	0.577 (1)	Longo & Anderson, 1969	egg has a jelly coat
Ligumia subrostrata	0.008 (1)	Trimble & Gaudin, 1975	unionid
Tapes decussatus	0.068 (1)	Pochon-Masson & Gharagozlou, 1970	venerid
Spisula solidissima	0.164 (1)	Longo & Anderson, 1969	
Nucula hartvigiana	0.033 (2)	Popham & Marshall, 1977	
Anadara trapezia	0.118 (6)	this paper	
Anomia descripta	0.036 (2)	this paper	
Fulvia tennuicostata	0.019 (2)	this paper	
Notocorbula vicaria	0.053 (2)	this paper	
Myodora brevis	0.018 (2)	this paper	

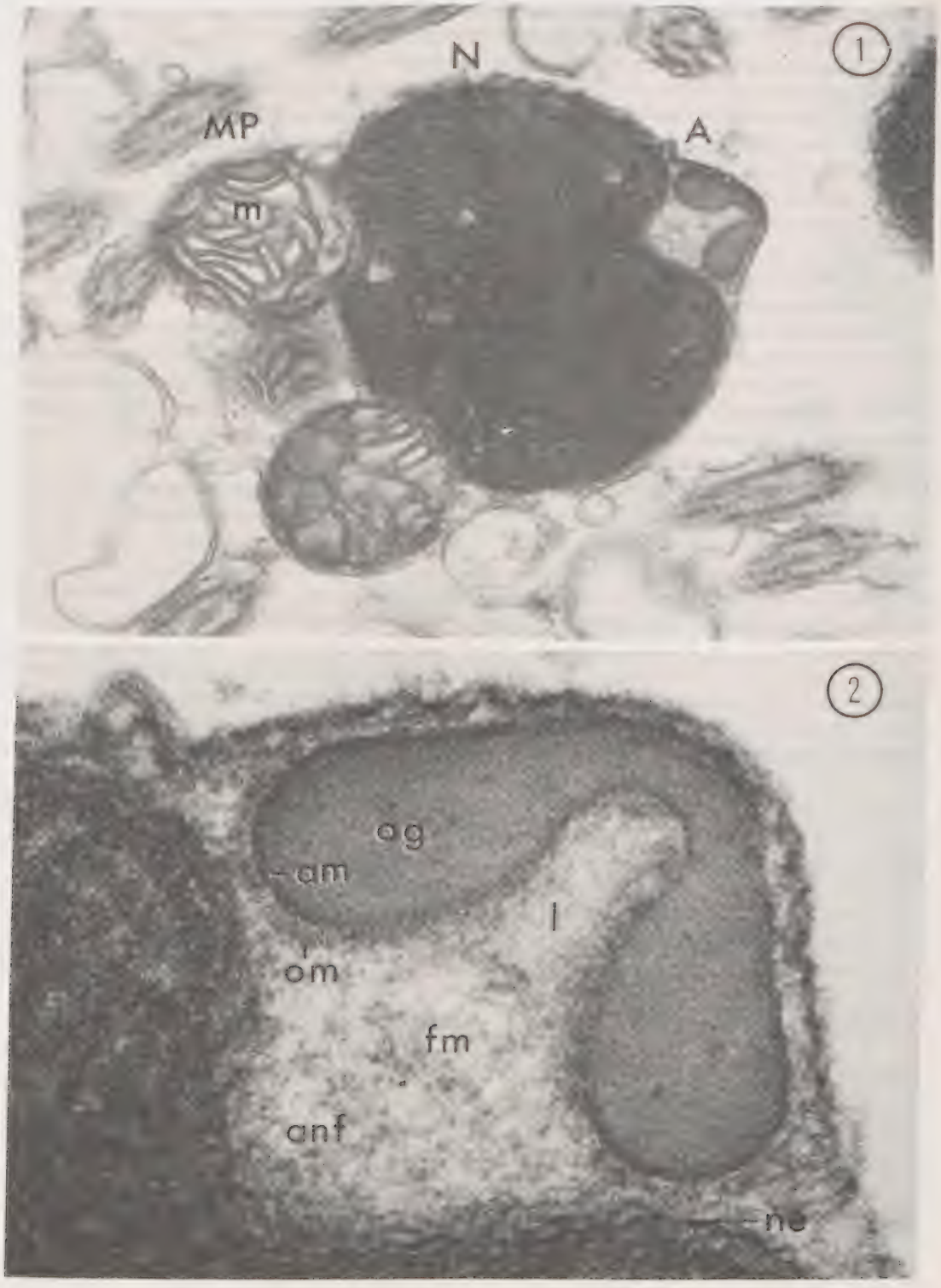


FIG. 1. *Anomia descripta*, longitudinal section. X37,000. FIG. 2. *Anomia descripta*, acrosome. X210,000. (See legend to Fig. 11 for key to labelling.)

RESULTS

Anomia descripta (Figs. 1, 2)

The sperm are approximately 2.2 μm long and have a spherical nucleus (N) capped by a small acrosome (A) at the anterior end and bounded by a middle piece (MP) at the posterior end. The nucleus has both an anterior nuclear fossa (anf) and a posterior nuclear fossa.

The acrosome consists of a membrane-bound, osmiophilic granule (og) which is homogeneous in appearance. The granule resembles a hollow cone and appears to be relatively small with a profile ratio equal to 0.036 (Table 2). The inner surface of the acrosomal membrane (am) is closely apposed to the granule. Its outer surface is covered with osmiophilic material (om). The membrane also appears to be close to the nuclear envelope (ne). The lumen of the acrosome (l) and anterior nuclear fossa form a single unit occupied by flocculent material (fm).

The middle piece of the sperm consists of 4 nearly spherical mitochondria (m) measuring about 0.69 μm in diameter. The mitochondria surround 2 centrioles oriented at 90° to each other.

Anadara trapezia (Figs. 3, 4)

The sperm are approximately 3.10 μm long. The nucleus is barrel-shaped and indented only with a posterior nuclear fossa (pnf).

The acrosome (A) consists of a cup-shaped, osmiophilic granule of homogeneous consistency and some vesicles (v) (the exact number of which appears to be variable) located within the lumen (l) surrounded by the granule. The acrosomal granule is not close to the nuclear envelope but instead, is separated from it by some flocculent material (fm). The profile ratio of the granule to the nucleus is 0.118 (Table 2).

The middle piece of the sperm consists of 5 mitochondria (although both 4 and 6 have been seen) each measuring about 0.72 μm in diameter, surrounding 2 centrioles oriented at 90° to each other. A satellite body can be seen attached to the proximal centriole (pc).

Fulvia tennuicostata (Figs. 5, 6)

The sperm are approximately 2.0 μm long. The nucleus (N) is spherical and indented with only a shallow post nuclear fossa (pnf). The anterior-most portion of the nucleus is evaginated into the acrosomal lumen (l).

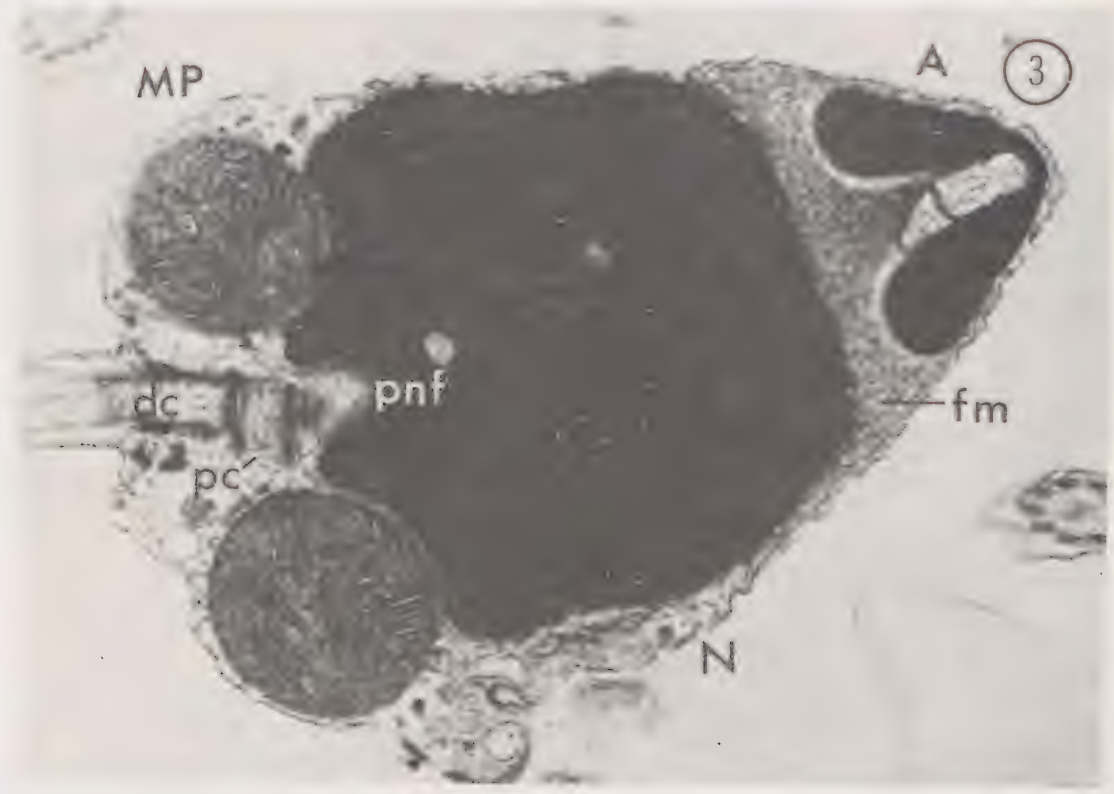
The middle piece (MP) consists of 4 spherical mitochondria (m), 0.56 μm in diameter, surrounding a pair of centrioles oriented at 90° to each other. Attached to the proximal centriole is a satellite body which also is inserted into the shallow post nuclear fossa (pnf).

The acrosome (A) consists of a ring-like osmiophilic granule (og). The profile ratio of the granule to nucleus is 0.019 (Table 2). The acrosomal membrane is folded into a U-shaped structure, the lumen (l) which is filled with flocculent material. The inner surface of the acrosomal membrane is lined by osmiophilic material (om). The acrosome does not appear to be close to the nuclear envelope, although the flocculent material appears to separate these 2 structures.

Notocorbula vicaria (Figs. 7, 8)

The sperm are 3.0 μm long. The nucleus (N) is conical, and has a shallow posterior nuclear fossa (pnf) but not an anterior one.

The middle piece (MP) consists of 4 mitochondria (m) which are depressed along the



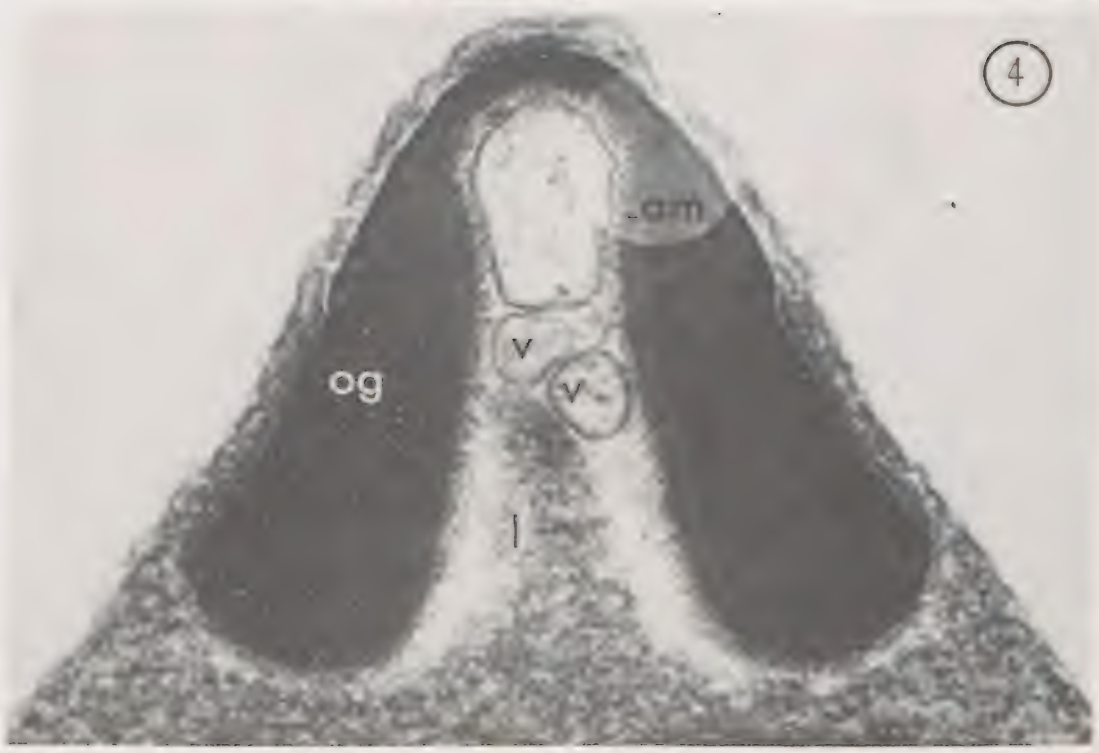


FIG. 3. *Anadara trapezia*, longitudinal section. X37,000. FIG. 4. *Anadara trapezia*, acrosome. X114,000.

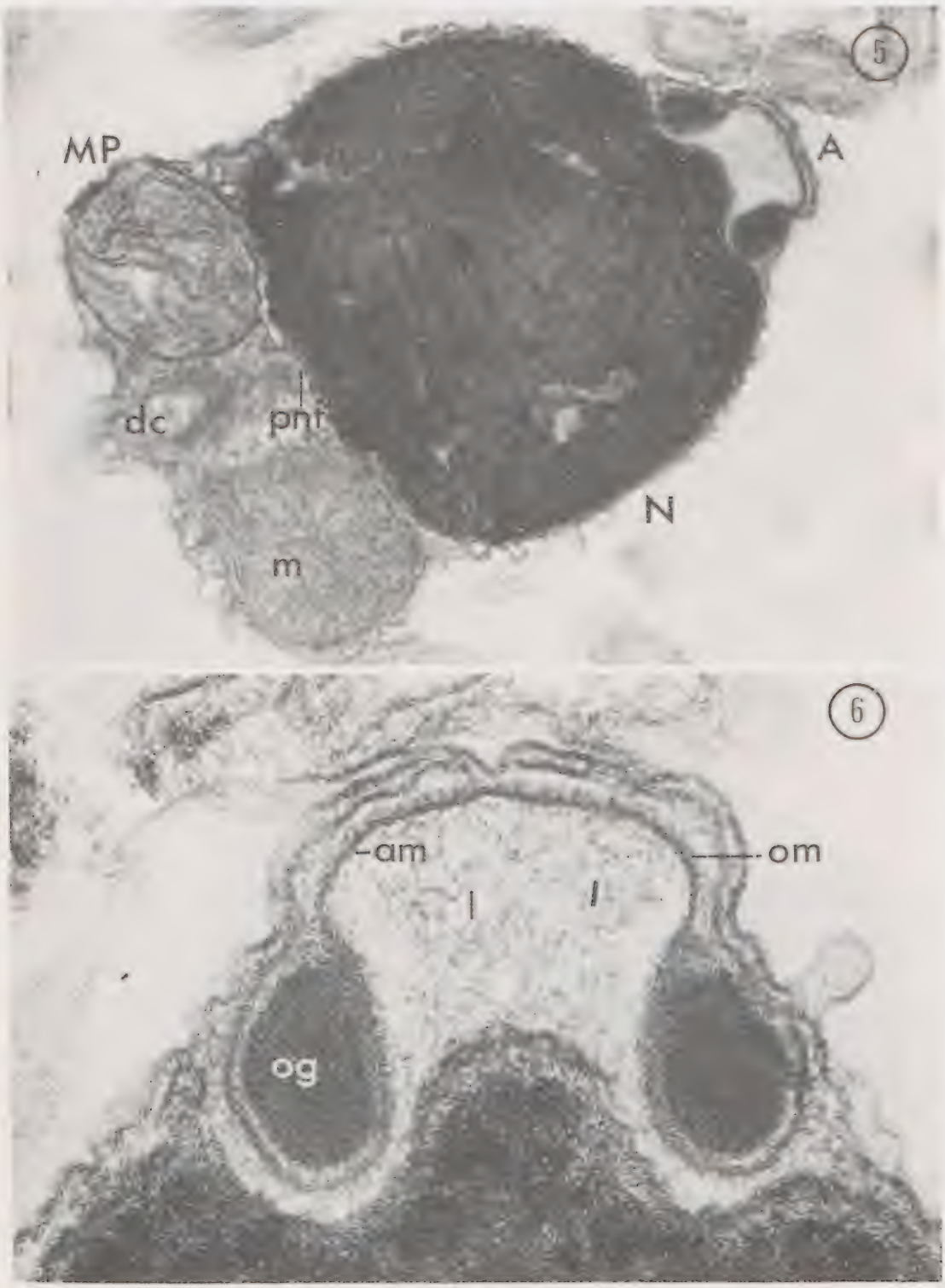


FIG. 5. *Fulvia tennuicostata*, longitudinal section through the sperm. X50,000. FIG. 6. *Fulvia tennuicostata*, acrosome. X171,000.

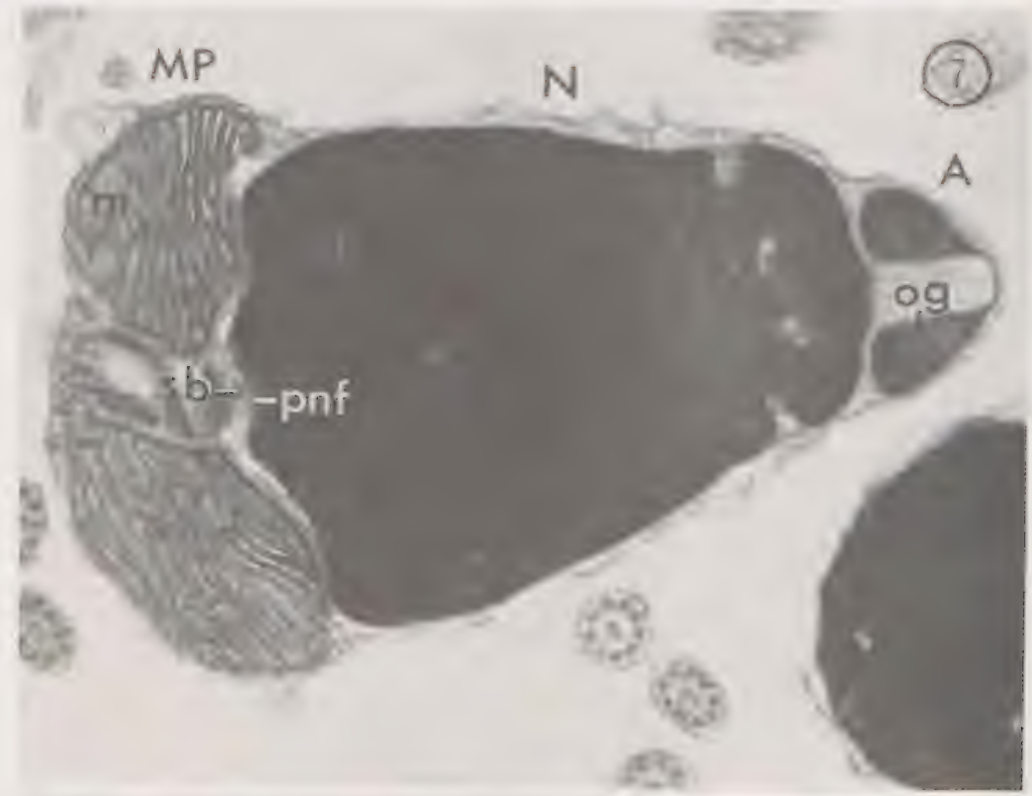


FIG. 7. *Notocorbula vicaria*, longitudinal section through the sperm. X37,000. FIG. 8. *Notocorbula vicaria*, acrosome. X130,000.

longitudinal axis of the sperm. The mitochondria surround a pair of centrioles oriented at 90° to each other. The proximal centriole has a satellite body (sb) which is inserted into the posterior nuclear fossa (pnf).

The acrosome (A) consists of a membrane-bound, osmiophilic granule (og), the shape of which can be described as resembling a hollow, truncated cone. The granule consists of two substances (Fig. 8), one of which stains very densely and resembles a ring-like structure (rog) and the other of which is less densely stained and occupies the remaining volume of the vesicle (rom). The profile ratio of the granule (taken as a whole) to the nucleus is 0.053 (Table 2). The acrosome is separated from the nuclear envelope by flocculent material. This same material appears to occupy the lumen (l) erected by the invagination of the inner acrosomal membrane (iam).

Myodora brevis (Figs. 9-11)

The sperm are unusual as the acrosome (A) is not found capping the nucleus (N) but rather is associated with the middle piece (MP). Their length, when measured from the base of the middle piece to the tip of the nucleus, is approximately 2.8 μm long. The nucleus is bullet-shaped and appears to have neither an anterior nor a posterior nuclear fossa.

The middle piece consists of 5 mitochondria (M) which, when viewed at right angles to the longitudinal axis, have generally circular profiles; when viewed down the length of the longitudinal axis, they have somewhat triangular profiles. The mitochondria surround a pair of centrioles which are oriented at 90° to each other.

The acrosome (A) consists of a membrane-bound, crescent-shaped, osmiophilic granule (og) and flocculent material lying within a lumen enclosed by the granule (l), 1 or 2 mitochondria, and the distal centriole (dc). The profile ratio of the granule relative to the nucleus is 0.018.

Observation on the formation of the acrosome during spermiogenesis has revealed that the single granule is formed at first in the anterior of the sperm. It would appear that toward the end of spermiogenesis when most of the cytoplasm has disappeared, the granule migrates posteriorly (see Fig. 11).

DISCUSSION

This study showed that the fine structure of the sperm of the marine-dwelling bivalves is far more variable than hitherto realized. This variability can be largely ascribed to variations in the morphology, composition and location of the acrosome within the spermatozoon, although variations in the morphology of the nucleus and morphology and number of mitochondria appear to occur within rather narrow limits. For example, as shown in this work, the nucleus can be spherical (*Anomia descripta*), ovoid (*Anadara trapezia*) or cylindrical (*Notocorbula vicaria*), as previously reported for other bivalve species (see Introduction). One feature of note, however, arising from this study is the absence of an anterior nuclear fossa in 4 of the 5 species sampled. It would appear that the presence of an anterior nuclear fossa can be correlated with the presence of an axial rod in the acrosome. The occurrence of a posterior nuclear fossa appears to be correlated with the presence of the satellite body of the proximal centriole.

As observed in the previously examined bivalves, the mitochondria in the sperm of the present species had largely circular profiles. Little significance can be attributed to the internal structure or configuration of these organelles (compare the mitochondria in Figs. 1 and 7, which have a condensed configuration, with those of Figs. 3 and 5, which have an orthodox configuration) as it may be dependent on a number of factors: concentration of

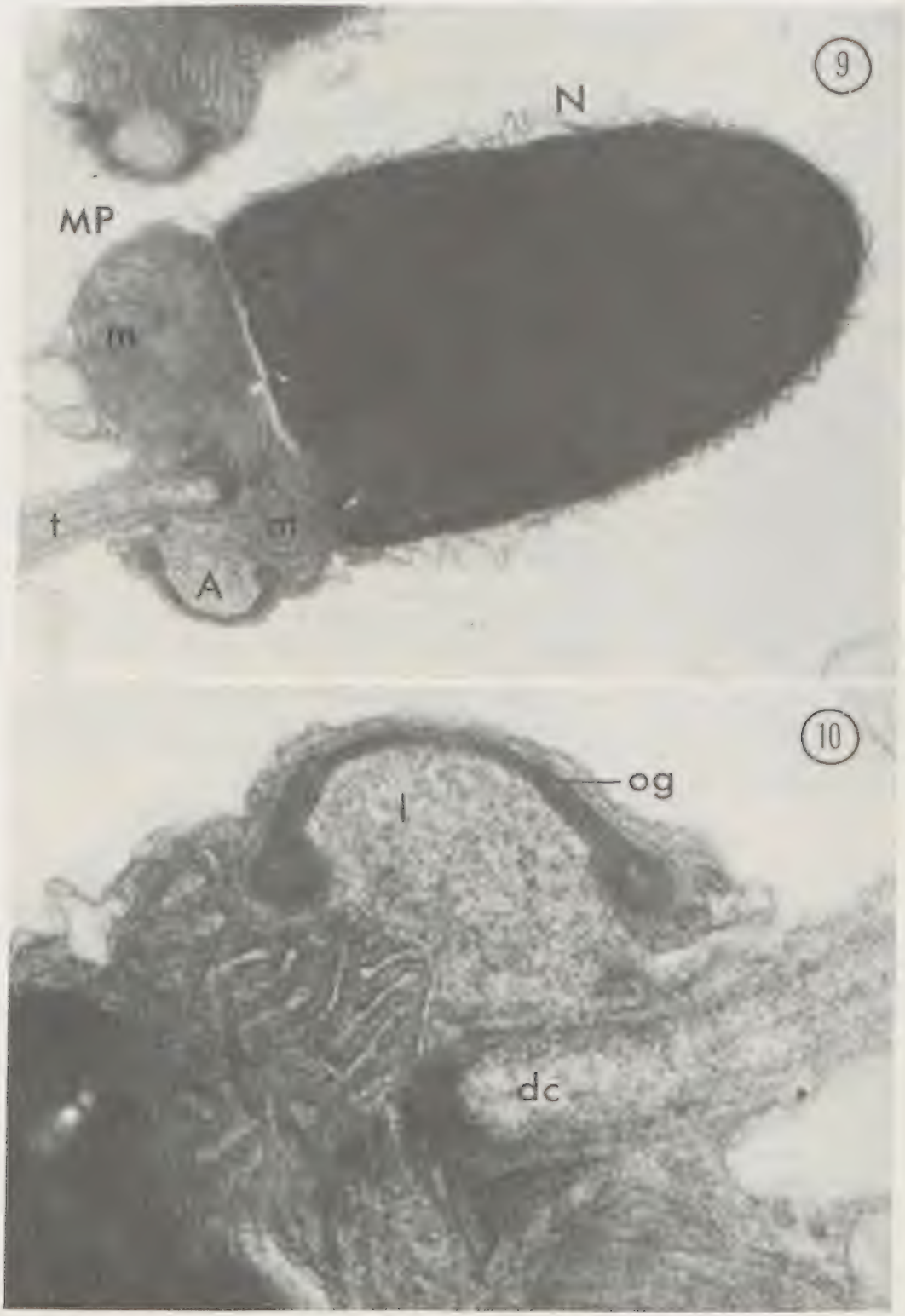


FIG. 9. *Myodora brevis*, longitudinal section through the sperm. X30,000. FIG. 10. *Myodora brevis*, acrosome and mitochondria. X86,000.

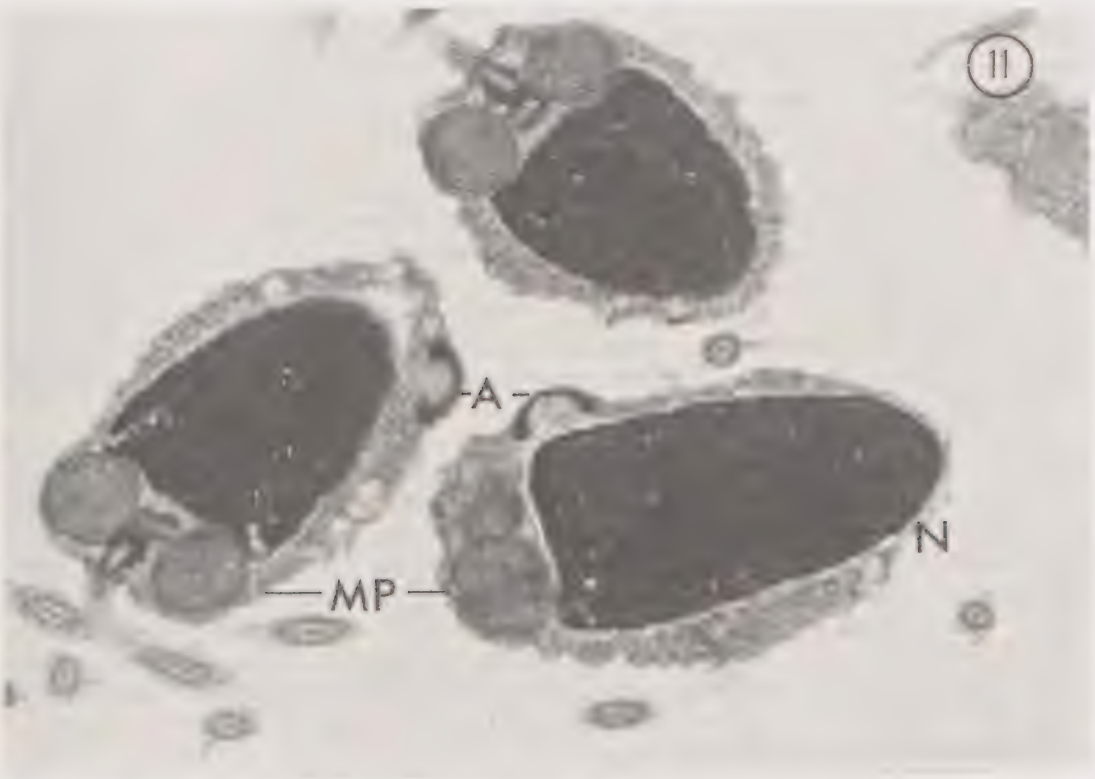


FIG. 11. *Myodora brevis*, late spermatids. X14,000.

Key to figure labels (Figs. 1-11). A, Acrosome; am, acrosomal membrane; anf, anterior nuclear fossa; dc, distal centriole; fm, flocculent material; iam, inner acrosomal membrane; l, lumen of invaginated vesicle; m, mitochondrion; MP, Middle Piece; ne, nuclear envelope; N, Nucleus; og, osmiophilic granule; om, osmiophilic material; pc, proximal centriole; sb, satellite body of proximal centriole; pnf, posterior nuclear fossa; t, sperm tail.

inorganic phosphate, ion transport, osmotic pressure of the medium, demand for oxygen, etc. (see review by Munn, 1974).

The variability in the size (weight), composition, morphology and position of the acrosome in the sperms of the present bivalves is astounding. The essential functions of the acrosome are to dissolve egg coats and permit fusion of the sperm plasma with the egg plasma membrane (see reviews by Colwin & Colwin, 1964, 1967; Dan, 1956, 1967; Franklin, 1970; Longo, 1973; Pasteels, 1965a,b). Hence, it is highly probable that some of the variation in the characteristics of the acrosome may reflect functional differences associated with egg coat structure (Nishiwaki, 1964; Baccetti, 1970) rather than random mutations which have been maintained in the species. For example, brooding teredines have smaller acrosomes than do non-brooding ones (Popham, 1974a). Similarly the large acrosome of the sperm of *Mytilus edulis* (Table 1) may be due to the fact that the eggs of this species are covered with a thick coat of jelly (Humphreys, 1962). A similar finding was found by Nishiwaki (1964) in regard to spermatozoa of the prosobranch gastropods. Species having thick egg coats had spermatozoa with large acrosomes and vice versa. When the profile ratios of the osmiophilic material within the acrosome are listed (Table 2) for the various species, it can be seen that there is an over 70-fold difference in values between the extremes, with a 15-fold difference in the species of the subclass Pteriomorphia alone. The reason for such large differences is presently not known.

The most consistent feature of the sperms investigated in this work is that they lack an axial rod as part of the apparatus making up the acrosome. Trimble & Gaudin (1975) reported a similar observation for the sperm of the unionid *Ligumia subrostrata*, and this same situation most likely also occurs in another unionid, *Hyriopsis schlegelii* (Higashi, 1964). In the unionids the acrosome is very small in that the acrosome to nucleus ratio is 2-14 times smaller than similar values for the spermatozoa just described in the account. Furthermore, since there appears to be no evidence to suggest that the species just described are brooders, it cannot be concluded that the absence of the axial rod may be in response to fertilization of the oocytes in the mantle cavity. Popham (1974b) speculated that the axial rod in the bivalve sperm may act as a support about which the inner acrosomal membrane is folded into a small radius of curvature, a factor promoting fusion of cell membranes (Bangham, 1964; Bangham & Pethica, 1960; Pethica, 1961; Weiss, 1964, 1967). This speculation may need revision in light of the present findings and those of Higashi (1964), Trimble & Gaudin (1975) and Popham & Marshall (1977).

As indicated in the introduction to this paper, the stimulus for observing the fine structure of the sperm of the bivalves was to see if the morphology of the sperm could be correlated with the phylogeny of the Bivalvia. More specifically, it was expected that the results would show that 2 pteriomorph species, *Anadara trapezia* and *Anomia descripta*, would have sperms with morphologies similar to those previously found for *Mytilus edulis* and *Crassostrea virginica*, especially in relation to the placement of the axial rod (see Popham et al., 1974). This work shows that the prediction was incorrect. Thus, in the Pteriomorphia at least, it is difficult to correlate sperm morphology with any particular phylogenetic tree (Cox, 1960; Morton, 1963; Stasek, 1963; Newell, 1965, 1969a) of the species of this subclass. Quite obviously the sperm of pterids and pectins need to be examined to obtain a better appreciation of what is happening.

At one time the structure of the ctenidia was used as a basis for assessing phylogenetic relationships among all the bivalves until it was realized that grades of the structure of the ctenidia evolved independently throughout the class (Newell, 1969a). It appears that the great extent of parallel or possible convergent evolution which has occurred in the Bivalvia has contributed much to impeding progress in solving the phylogenetic relationships among the species (Newell, 1969a; Cox et al., 1969). Hence, the apparent absence of axial rods in the sperms of some heterodont species, viz., *Fulvia tennuicostata* and *Notocorbula vicaria* (some pteriomorph species and a paleotoxodont species; Popham & Marshall, 1977), hints at the possibility that axial rod formation may have evolved independently in the Pteriomorphia and Heterodonta, especially when Franzen's (1956) observation of similar structures arising in the acrosome of unrelated species is remembered. With this point in mind, it would appear that 4 patterns of placement of the acrosome in the sperms of the Bivalvia occur (Fig. 12). It would further seem that the absence of an axial rod is the only consistent feature of the 4 patterns. It is possible, however, that the small or non-existent acrosome in the unionids precludes the presence of an axial rod. Hence, its absence in the order Unionoida may be a secondary adaptation. It is for this reason that a question mark has been placed above the sperm representing the Paleoheterodonta in Fig. 12. The sperm in question may only represent the order Unionoida. The sperm of species of the order Trigonioida may be quite different. Nevertheless, it seems likely that the absence of an axial rod in the acrosome represents the primitive bivalve condition, especially since no axial rod is found in *Nucula hartvigiana* (Popham & Marshall, 1977).

The finding of an acrosomal vesicle migrating from the anterior end of the sperm of *Myodora brevis* to become close to the middle piece is in agreement with a similar finding by Retzius (1905) and Franzen (1955) for *Lyonsia norvegica*. Both genera have been ascribed to the superfamily Pandoracea (Newell, 1969b). Atwood (1975) reported an analogous situation for the sperm of the brooding holothoridian, *Cucumaria pseudocurata*. Hence, it

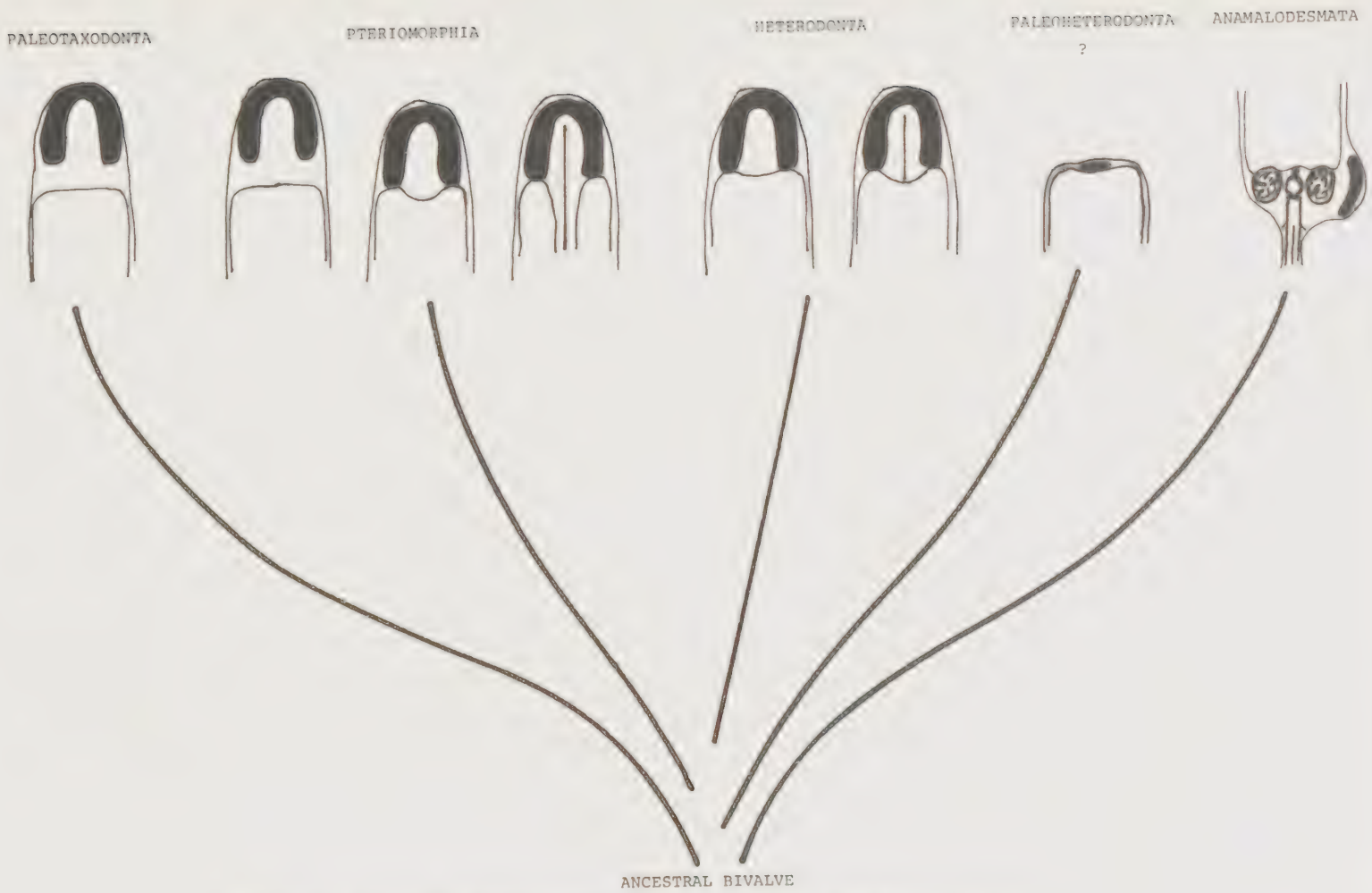


FIG. 12. Summarised findings on sperm morphology within 5 subclasses of the Bivalvia.

may be possible that both *M. brevis* and *L. norvegica* are brooders. But how the sperms fertilize the eggs remains an intriguing question.

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J. DAVID POPHAM

Department of Anatomy
University of Sydney
Sydney, New South Wales, Australia

Malacological Review, 1979, 12: 21-28

HERMAPHRODITISM IN *ELLIPTIO* (PELECYPODA: UNIONIDAE)[1]

William H. Heard

ABSTRACT

The gonadal organizations and the spacings of interlamellar septa are described for 22 monoecious animals found among 1026 *Elliptio arctata, E. buckleyi, E. complanata* and *E. icterina* examined histologically. Samples of 152 *E. crassidens* s.s., *E. c. downiei, E. hopetonensis, E. jayensis* and *E. mcmichaeli* contained only males and females.

The gonads of a total of 18 hermaphroditic *Elliptio arctata, E. buckleyi, E. complanata* and *E. icterina* contained a preponderance of testicular tissue, and those of four *E. complanata* and *E. icterina* contained about as much or more ovarian tissue. Eleven *E. arctata, E. buckleyi, E. complanata* and *E. icterina* had intermingled zones of male and female acini, and 10 animals of these same four species had regionally distinct and separate male and female acini; one *E. icterina*, with a preponderance of testicular tissue, had a few monoecious acini.

Outer, marsupial demibranchs of females had about 3-10 filaments on each side of the water-tubes (short), and non-marsupial demibranchs of females and males had about 20 filaments (long water-tubes). The hermaphrodites possessed eight different combinations of gonadal constitution and sizes of water-tubes (long, intermediate and short) in the four demibranchs, and gravid animals displayed two of those combinations.

The cause(s) of the variable expressions of hermaphroditism in *Elliptio* are unknown, but the low frequencies of monoecious animals indicate that hermaphrodites do not contribute significantly to reproduction within their populations.

INTRODUCTION

Van der Schalie (1970) found only males and females among six *Elliptio buckleyi* (Lea), five *E. complanata* (Lightfoot), 22 *E. crassidens* (Lamarck), eight *E. fraterna* (Lea), six *E. strigosa* (Lea) [=*E. arctata* (Conrad), *fide* Johnson (1970)], and six *E. tuomeyi* (Lea) [=*E. icterina* (Conrad), *fide* Johnson (1970)], but reported two hermaphrodites among 68 *E. dilatata* (Rafinesque) and one hermaphrodite among nine *E. productus* (Conrad) [=*E. lanceolata* (Lea), *fide* Johnson (1970)].

The ovotestes of both monoecious *Elliptio dilatata* consisted predominantly of ovarian tissue with some hermaphroditic acini being present, and one of the animals was gravid, whereas the non-gravid monoecious *E. productus* contained a preponderance of testicular tissue (interpretations from legends to van der Schalie's (1970) figs. 5-7). However, it is unknown whether the outer demibranchs of these three animals were of marsupial or non-marsupial structural organization, i.e., possessed either densely spaced interlamellar septa and therefore longitudinally short water-tubes (interlamellar spaces) or distantly spaced septa and long water-tubes, respectively.

The only other reported case of hermaphroditism in this genus was one predominantly ovarian animal among 150 *Elliptio complanata* (Matteson, 1948); details of demibranch organization were not given, nor was it noted whether the animal was gravid.

Hermaphroditism in freshwater mussels is seemingly most widespread in the unionid subfamily Anodontinae Ortmann, and especially so in *Anodonta* Lamarck (see van der Schalie, 1970; Heard, 1975). Bloomer (1934) reported that in *A. cygnea* (Linnaeus) in England the structure of an individual's outer demibranchs was not always correlated with the nature of

[1]This investigation was supported, in part, by contract 14-16-008-8760 from the Office of Endangered Species, U.S. Fish and Wildlife Service.

the gonads, and he concluded that sex-reversal occurs in that species. In contrast, Heard (1975) found that in several North American *Anodonta* the outer demibranchs were always marsupial in females and "female-hermaphrodites" (ovarian tissue approximating or greatly exceeding the amount of testicular tissue) and always non-marsupial in males and "male-hermaphrodites" (predominance of testicular tissue). In addition, female-hermaphrodites were found in gravid condition, but male-hermaphrodites were never gravid.

The purposes of this report are to record additional occurrences of hermaphroditism in *Elliptio* Rafinesque, and to provide a description of the nature of the gonads and structure of the demibranchs in the monoecious animals.

MATERIAL EXAMINED

Elliptio arctata (Conrad). North Mosquito Creek adjacent to Florida State Hospital, Chattahoochee, Gasden County, Florida. Animals from 12 consecutive monthly collections: June 1976 to May 1977. 62 ♂, 60 ♀ and 4 ⚥.

Elliptio buckleyi (Lea). Myakka River at Myakka River State Park, about 27 km southeast of Sarasota, Sarasota Co., Fla. Six bimonthly collections: January, March, May, July, September and November 1965. 26 ♂, 30 ♀ and 3 ⚥.

Elliptio complanata (Lightfoot). Spring Creek at Federal Highway 90, 3.2 km southeast of Marianna, Jackson Co., Fla. Thirteen consecutive monthly collections: March 1976 to March 1977, each with two forms: shell of *form A* posteriorly inflated and with incurved ventral margin (67 ♂, 71 ♀ and 2 ⚥), and shell of *form B* compressed and with rather straight or slightly convex ventral margin (62 ♂, 62 ♀ and 2 ⚥).

Elliptio crassidens crassidens (Lamarck). Population 1: Apalachicola River at Chattahoochee, Gadsden Co., Fla.; 14 May 1977 (9 ♂ and 15 ♀). Population 2: Chipola River at State Road 167, 1.6 km north of Marianna, Jackson Co., Fla.; 16 November 1973 (3 ♂ and 7 ♀).

Elliptio crassidens downiei (Lea). Satilla River at Federal Highway 301, 4.8 km south of Hortense, border of Wayne and Pierce counties, Georgia; 11 October 1973. 14 ♂ and 16 ♀.

Elliptio hopetonensis (Lea). Ohoopee River at State Road 56, 3 km southwest of Covena, Treutlen Co., Georgia; 25 October 1973. 17 ♂ and 15 ♀.

Elliptio icterina (Conrad). Population 1: Little (= South Prong of) St. Marys River at Federal Highway 90, 1.6 km west of Macclenny, Baker Co., Fla.; 10 December 1973 and 10 May 1974 (25 ♂, 26 ♀ and 3 ⚥). Population 2: same North Mosquito Creek locality as for *E. arctata*; 19 consecutive monthly collections: April 1976 to September 1977 (107 ♂, 101 ♀ and 3 ⚥). Population 3: Steinhatchee River at Federal Highway 19, 26.4 km northwest of Cross City, border of Dixie and Taylor counties, Fla.; monthly collections from March 1976 to April 1977, except in January and February (154 ♂, 151 ♀ and 5 ⚥).

Elliptio jayensis (Lea). Black Creek at State Road 209, 10.7 km northwest of Green Cove Springs, Clay Co., Fla.; 16 October 1977. 11 ♂ and 9 ♀.

Elliptio mcmichaeli Clench & Turner (? = *E. fraterna sensu* van der Schalie, 1970). Choctawhatchee River at State Road 20, Ebro, border of Walton and Washington counties, Fla.; 20 November 1971. 20 ♂ and 16 ♀.

Shells from each of these populations have been deposited as voucher specimens in the Museum of Comparative Zoology, Harvard University.

METHODS

The animals described herein were discovered during a survey of seasonal gonad activity in the *Elliptio* in the Mosquito, Myakka, Spring and Steinhatchee localities, findings on which will be published elsewhere. Five animals with provisionally identified marsupial outer demibranchs and five with non-marsupial outer demibranchs were taken from each monthly collection, and sections of the gonads were made from each of these individuals. Frontal sections of the outer and inner demibranchs of several known males and females, and of each hermaphrodite, were made. In order to assess the accuracy of identification of the kind of outer demibranch, the gonads of all 310 individuals of Steinhatchee River *E. icterina* were sectioned, as were those of all animals from the other sites not named above. Histological sections of gonads and demibranchs were prepared according to the methods used by Heard (1975).

Septal spacing was determined by counting the number of ordinary filaments along the sides of water-tubes, i.e., between consecutive interlamellar septa. Demibranchs with comparatively low numbers of filaments per water-tube were considered to be marsupial, and those with comparatively high numbers were treated as non-marsupial.

FINDINGS

Gonadal constitution

Just 22 of the 1178 individuals examined histologically, viz., 1.87%, were monoecious (see Table 1). The gonads of 18 of those hermaphrodites contained predominantly testicular tissue (Fig. 1), whereas four contained about as much or more ovarian tissue (Fig. 2). In 16 animals the kind of gonadal tissue that was least abundant lagged in gametogenic development (Fig. 3). The six exceptions are: four animals in which the least abundant gonadal tissue was of more advanced development, viz., those with much ovarian tissue; one in which both kinds of tissue were of equal development; and one in which the most abundant kind was the most developed. Fifteen of the 22 hermaphrodites were found during the breeding season of the specific populations, although the relative states of development of the two kinds of gonadal tissue were not consistently related to the time of year.

Eleven hermaphrodites had intermingled zones of male and female acini, and 10 displayed regionally distinct and separate male and female acini (see Table 1). *Elliptio complanata* form A showed only the former condition, whereas form B had just the latter; *E. arctata, E. buckleyi* and all three populations of *E. icterina* contained animals of both conditions. The single animal with monoecious acini contained a vast predominance of testicular tissue, with eggs present in just four adjacent acini (Fig. 4).

Demibranch structure

Frontal sections of female outer demibranchs confirmed Ortmann's (1911) report of unipartite marsupial organization in *Elliptio*, i.e., of simple, vertically undivided interlamellar septa and water-tubes. The non-marsupial demibranchs, viz., the inner ones of females and all four in males, were also of unipartite organization, although they were distinguished from the marsupial demibranchs by more distantly spaced septa and therefore longitudinally longer water-tubes that were flanked on each side by a greater number of filaments. Marsupial water-tubes had about three to five filaments on each side in *E. arctata, E. buckleyi, E. complanata* (both forms), *E. icterina* and *E. jayensis*, and about 7-10 in *E. crassidens* s.l., *E. hopetonensis* and *E. mcmichaeli*; non-marsupial water-tubes of all species had about 20 filaments on each side (Table 2).

All demibranchs of all hermaphrodites were likewise of unipartite structure, but septal spacing varied more in them than in males and females. Eleven hermaphrodites had long water-tubes in all four demibranchs: one *Elliptio buckleyi*, four *E. complanata* (two of each form), one Little St. Marys River *E. icterina*, three Mosquito Creek *E. icterina* and two Steinhatchee River *E. icterina*; all of these animals except one each of the two forms of *E. complanata* contained mostly testicular tissue (Table 1). Three other hermaphrodites had short water-tubes in the outer demibranchs and long water-tubes in the inner demibranchs: one *E. arctata* with mostly testicular tissue, and two Little St. Marys River *E. icterina* with much ovarian tissue. The remaining seven monoecious animals, all with predominantly male gonads, had intermediate-sized water-tubes in the outer demibranchs; four of them also had intermediate-sized water-tubes in the inner demibranchs (one *E. arctata*, two *E. buckleyi* and one Steinhatchee River *E. icterina*), and three had long water-tubes in the inner demibranchs (one *E. arctata* and two Steinhatchee River *E. icterina*).

TABLE 1. Relative proportions of testicular and ovarian tissue in each hermaphroditic *Elliptio* examined, and the number of filaments (mean ± 1 standard deviation) along each side of the water-tubes in different demibranchs of those individuals. Ten water-tubes were studied in each demibranch. LSMR: Little St. Marys River; MC: Mosquito Creek; SR: Steinhatchee River.

Species	Spn.	% of gonads		Outer demibranchs		Inner demibranchs	
		Testicular	Ovarian	Mean ± S.D.		Mean ± S.D.	
E. arctata	1[r]	>95	<5	11.70	3.16	17.50	1.90
	2[i]	>95	<5	3.80	0.63	15.30	2.00
	3[r,d]	>95	<5	–	–	–	–
	4[r]	>95	<5	9.00	1.56	13.60	2.01
E. buckleyi	1[r]	>95	<5	17.00	2.87	16.80	4.52
	2[i]	>95	<5	7.70	1.16	12.00	3.06
	3[i]	>95	<5	11.30	1.70	9.70	1.06
E. complanata							
form A	1[i]	25	75	19.50	2.27	18.80	2.57
	2[i]	>95	<5	18.40	3.86	19.40	3.03
form B	1[r]	>95	<5	21.10	2.47	19.30	2.26
	2[r,g]	<5	>95	21.10	2.85	20.20	3.33
E. icterina							
LSMR	1[i]	55	45	7.10	1.73	20.50	2.99
	2[r]	>95	<5	19.40	1.58	20.30	3.53
	3[r,g]	<5	>95	5.50	1.35	19.80	1.69
MC	1[m]	>95	<5	19.60	4.97	20.30	3.06
	2[i]	>95	<5	20.80	3.26	20.40	3.75
	3[i]	>95	<5	20.40	3.17	20.20	4.21
SR	1[i]	>95	<5	19.10	1.79	19.50	1.65
	2[i]	>95	<5	19.50	2.51	17.70	4.19
	3[i]	>95	<5	10.90	2.02	19.00	3.65
	4[r]	75	25	9.20	1.62	20.00	4.64
	5[r]	>95	<5	10.40	1.71	11.80	2.04

[d]Discarded before demibranchs could be examined.

[g]Gravid.

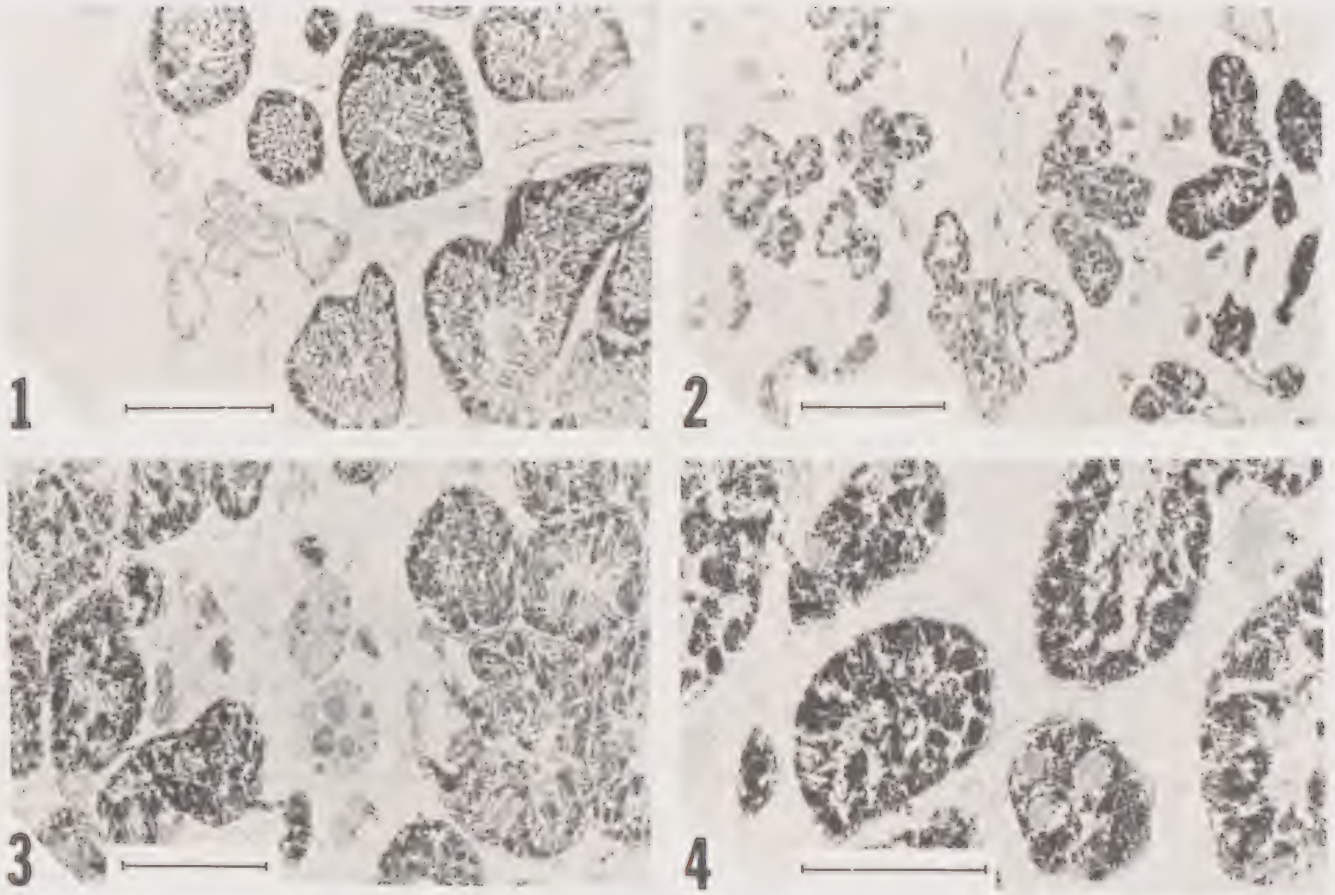
[i]Intermingled zones of male and female acini.

[m]With a few monoecious acini.

[r]Regionally distinct and separate male and female acini.

TABLE 2. Number of filaments (mean ± 1 standard deviation) along each side of the water-tubes in different demibranchs of female and male *Elliptio*; 30 water-tubes were studied for each condition. AR: Apalachicola River; CR: Chipola River; other abbreviations as in Table 1.

Species	Outer demibranchs		Inner demibranchs	
	Female	Male	Female	Male
	Mean ± S.D.	Mean ± S.D.	Mean ± S.D.	Mean ± S.D.
E. arctata	3.30 1.15	19.70 2.32	19.70 2.60	19.07 2.62
E. buckleyi	3.33 0.76	19.17 3.63	16.13 2.84	17.73 4.18
E. complanata				
form A	3.57 1.22	19.10 2.41	18.40 2.03	19.40 2.72
form B	4.53 1.43	20.10 3.00	20.53 2.84	20.90 3.61
E. crassidens s.s.				
AR	8.47 1.48	18.87 3.03	21.43 3.33	18.10 3.53
CR	10.50 2.27	22.57 3.95	23.57 3.40	24.67 2.76
E. c. downiei	6.83 1.58	19.67 3.53	20.70 4.06	20.00 4.03
E. hopetonensis	8.07 1.78	21.87 3.96	20.60 3.48	21.50 3.31
E. icterina				
LSMR	4.97 1.71	20.47 3.77	19.67 3.18	21.67 2.91
MC	2.80 1.00	19.87 2.03	21.00 3.21	20.03 2.65
SR	4.20 1.10	20.63 3.15	19.50 2.15	20.20 3.12
E. jayensis	5.47 1.28	19.23 2.64	19.97 3.64	18.90 3.11
E. mcmichaeli	8.43 1.76	20.17 3.76	20.27 4.45	20.20 4.11



FIGS. 1-4. Photomicrographs of hermaphroditic gonads in *Elliptio*. FIG. 1. *E. arctata* with predominantly testicular tissue (see Table 1: specimen 3). FIG. 2. *E. complanata* form A with much ovarian tissue (Table 1: spn. 1). FIG. 3. Steinhatchee River *E. icterina* with least abundant, ovarian tissue lagging behind testicular tissue in gametogenic development (Table 1: spn. 2). FIG. 4. Mosquito Creek *E. icterina* with a few monoecious acini in a predominantly testicular individual (Table 1: spn. 1). Scale in Figs. 1-3: 50 μm; and in Fig. 4: 20 μm.

DISCUSSION

Van der Schalie's (1970) two monoecious *Elliptio dilatata* were, according to the criterion of gonadal constitution (= "visceral sex" *sensu* Heard, 1975), female-hermaphrodites; in addition, each contained some hermaphroditic acini, a state found here in one Mosquito Creek *E. icterina* with mostly testicular tissue. His monoecious *E. productus* was a gonadal male-hermaphrodite, seemingly with intermingled zones of male and female acini. That state occurred here in a total of 11 individuals. Regionally distinct and separate male and female acini, found in 10 animals, constitute a condition hitherto known only in *Anodonta imbecilis* Say among all other ectobranchous freshwater mussels (= Unionidae *sensu* Heard & Guckert, 1970).

Mature eggs and sperm were not simultaneously present in any of the 22 monoecious animals described herein, and thus none could be termed functional hermaphrodites *sensu* Coe (1943). All of the animals were "occasional", "partial" and "sporadic" hermaphrodites *sensu* van der Schalie (1966, 1970).

Unlike that in the investigated North American *Anodonta*, septal spacing in the outer demibranchs of monoecious *Elliptio* was not consistently correlated with gonadal constitution. As a consequence, a wide range of monoecious conditions is now known in *Elliptio*: (1) nine gonadal male-hermaphrodites had distantly spaced septa and thus long water-tubes in all four demibranchs, i.e., were evidently functional males, and (2) two gonadal female-hermaphrodites had densely spaced septa in the outer demibranchs and distant septa in the inner demibranchs, i.e., would seem to have the capacity to function as both male and female. The remaining hermaphrodites displayed four combinations of gonadal constitution and septal spacing: (3) mostly testicular tissue and intermediate septal spacing in all four demibranchs; (4) mostly testicular tissue, intermediate septal spacing in the outer demibranchs, and distant septal spacing in the inner demibranchs; (5) mostly testicular tissue, dense septa in the outer demibranchs and distant septa in the inner demibranchs; and (6) much ovarian tissue and distant septa in all four demibranchs. Moreover, there are two kinds of animals with monoecious acini: (7) one with mostly testicular tissue and (8) one with predominantly ovarian tissue. Finally, it is possible for hermaphroditic *Elliptio* with either (9) marsupial or (10) non-marsupial outer demibranchs to be gravid.

The monoecious state has been suggested to occur more commonly in cases of existence in standing waters (Weisensee, 1916), restricted contact with potential breeding partners (Cole, 1954; Ghiselin, 1969), small, genetically isolated populations (Ghiselin, 1969), beneficial size dimorphism between different sexes (Ghiselin, 1969), survival and dispersal advantage if the individual has the capacity for autofecundation (Heard, 1975). Although Heard (1975) found a greater frequency of monoecious *Anodonta peggyae* Johnson in flowing water, there is available concerning freshwater mussels little or no other empirical information bearing on these postulates. In terms of size, however, it was noted in this study that large male *Elliptio icterina* from Mosquito Creek were more frequent than females of the same size class. The hermaphrodites in all species (and populations) were of large size, and the condition was not confined to smaller individuals that might have been undergoing sex-reversal.

The detection of hermaphroditic freshwater mussels might be a matter of chance, or it could reflect relative commonness of the condition. Whether van der Schalie's (1970) finding of one gravid female-hermaphrodite in a sample of just three *Lasmigona complanata* (Barnes) truly indicates that monoecious animals are more common in that species than in Steinhatchee River *Elliptio icterina* (only five hermaphrodites among 310 individuals examined) is a moot question. Hermaphrodites were not found here in *E. crassidens* s.l., *E. hopetonensis, E. jayensis* and *E. mcmichaeli*, but such animals, if rare, might occur in larger samples.

The low frequencies of hermaphrodites in *Elliptio arctata*, *E. complanata* and *E. icterina* suggest that those animals play an insignificant role in contributing to breeding in their populations. Still, the existence of hermaphroditism and the cause(s) of it are curious. To better understand sexual expression in hermaphrodites, it will first be necessary to determine the mechanism of sex determination and expression in dioecious animals.

ACKNOWLEDGEMENTS

I express deep appreciation to V.A. Vail of the Tall Timbers Research Station, Tallahassee, for assistance in obtaining many of the animals upon which this report is based.

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WILLIAM H. HEARD

Department of Biological Science
Florida State University
Tallahassee, Florida 32306, U.S.A.

Malacological Review, 1979, 12: 29-36

THE TYPES OF UNIONACEA (MOLLUSCA: BIVALVIA) IN THE MUSEUM OF ZOOLOGY, THE UNIVERSITY OF MICHIGAN

Richard I. Johnson

The authors of unionid taxa most closely associated with the Museum of Zoology are Bryant Walker, Calvin Goodrich and Henry van der Schalie. References to all of their unionid types are included here, as well as all those of William A. Marsh, even if the specimens are located elsewhere. Lorraine S. Frierson and Bryant Walker purchased the Marsh collection and divided it. Later, Walker purchased the Frierson collection and the Marsh material was reunited.

In addition to the types of Frierson, Goodrich, Marsh, van der Schalie and Walker, the collection contains types of taxa described by Athearn, F. C. Baker, H.B. Baker, Bartsch, Call, Clench and Turner, Daniels, Dupuy, Gould, R.I. Johnson, Lea, Ortmann and Walker, Pilsbry, Pilsbry and Bequaert, Simpson, Tomlin, Wilson and Clark, S.H. Wright, and Wheeler.

SOME OF THE ASSEMBLAGES OF TYPES

Anthony, J.G. – Turner (1946) listed all of the taxa Anthony introduced and located all of his figured holotypes of Unionidae in the Museum of Comparative Zoology, Harvard University, as did Johnson (1956). Paratypes of some of Anthony's species, from the latter institution, are in The University of Michigan collection.

Baker, F.C. – F.C. Baker's types were studied by Franzen (1956, 1957, 1958), who located them in the University of Illinois, the Chicago Academy of Sciences and the University of Wisconsin. The types in the latter institution were subsequently transferred to the Museum of Zoology, The University of Michigan. Many of these were described in Baker's (1928) work on the freshwater mollusks of Wisconsin. References are included here to the holotypes or lectotypes selected by Franzen, with their present catalogue numbers. Franzen was not always consistent in the use of type categories, sometimes referring to figured allotypes (or paratypes) as syntypes even when a holotype had been selected. Sometimes paralectotypes were referred to as syntypes even after lectotypes had been chosen.

Baker, H.B. – The holotypes of all the Unionidae described by H.B. Baker from the University of Michigan-B. Walker expedition to Vera Cruz, Mexico (1922) and the University-Williamson expedition to Venezuela (1930) were located.

Bartsch, P. – Ruhoff (1973) studied Bartsch's types. One of his unionid species, *Nephronaias flucki*, is in the Museum of Zoology.

Call, R.E. – Call's types were studied by Johnson (1975a). A number of Call's paratypes and paralectotypes, received from the Museum of Comparative Zoology, are included here.

Frierson, L.S. – Frierson described 47 species of Unionidae and introduced a number of subgenera. His taxa were studied by Johnson (1972), who located the available holotypes and selected lectotypes for those known only from syntypes. The Museum of Zoology has 18 of these holotypes or lectotypes, as well as paratypes or paralectotypes of a number of the other species.

Goodrich, C. – Goodrich's types were studied by Rosewater (1959). Goodrich described one unionid, *Pleurobema aldrichianum.*

Gould, A.A. – Johnson (1964) studied Gould's types. Included here are paratypes of some of Gould's species received from the Museum of Comparative Zoology.

Lea, I. – Of the 851 species of Recent and fossil unionids described by Lea (Johnson, 1974), the Michigan collection has in it one suspected paratype of *Unio cromwelli* from J. Lewis and one paratype of *Unio forsheyi* from Anthony which Lea used in the original description.

Marsh, W.A. – Marsh introduced 10 unionid taxa (Johnson, 1975b); the holotypes or lectotypes of six of these are in the Academy of Natural Sciences of Philadelphia (Johnson & Baker, 1973), and two are in the University of Michigan's Museum of Zoology. Two others which should be there are missing. There is a syntype of one of these in the Museum of Comparative Zoology (Johnson, 1956: 140). References to all of the taxa are included here.

Ortmann, A.E. – Ortmann's types were studied by Johnson (1977). Most of his unionid types are in the Carnegie Museum, Pittsburgh.

Pilsbry, H.A. – Clench & Turner (1962) listed most of Pilsbry's taxa. Paratypes of two of his species, *Lampsilis semirasa* and *Mutela langi*, the latter described with Bequaert, are included here.

Simpson, C.T. – Simpson's unionid types, mostly in the National Museum of Natural History, were studied by Johnson (1975c). The holotype of one, *Pleurobema avellana*, was located in the Walker collection; another, *Quadrula flexuosa*, which should have been in the Frierson collection, could not be found.

van der Schalie, H. – References to all of the unionid species van der Schalie has described to date are included.

Walker, B. – Goodrich (1939) wrote a bibliography of Walker. References to all of Walker's unionid taxa are included in the present paper.

Wright, S.H. – The types of all of the taxa introduced by B.H. and S.H. Wright were refigured by Johnson (1967). Though only a paralectotype of *Unio brimleyi* was located, other paratypes or paralectotypes may still be in the Museum of Zoology's general collection.

A LIST OF THE TYPES OF UNIONACEA IN THE MUSEUM OF ZOOLOGY, THE UNIVERSITY OF MICHIGAN, WITH THEIR ORIGINAL REFERENCES AND TYPE LOCALITIES

The following list is arranged alphabetically by species, giving the author, year and place of publication of the original description, the type locality, and includes references to the location of the holotypes or lectotypes. If the holotype or lectotype is the the Museum of Zoology, paratypes there are not usually also included. All of the unionid taxa introduced by Goodrich, Marsh, van der Schalie and Walker are included here no matter where the types are located. All locality data in brackets are additions to already published records and are from original labels or modern atlases.

The following abbreviations have been used in this list: ANSP, Academy of Natural Sciences of Philadelphia, Pennsylvania; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; UMMZ, Museum of Zoology, The University of Michigan, Ann Arbor, Michigan; USNM, National Museum of Natural History, Washington, D.C.

aldrichi Frierson, *Pleurobema*: 1927, *Check list N. Amer. naiades*, p 44 ([Alabama River] Selma [Autauga Co.], Alabama). Lectotype ANSP 145246 selected by Johnson, 1972, *Occas. Pap. Moll.*, 3: 141, pl. 24, fig. 2; paralectotypes presumed to be in the UMMZ, but not located.

aldrichianum Goodrich, *Pleurobema*: 1931, *Occas. Pap. Mus. Zool., Univ. Mich.*, (229): 1-4, pl. 1 (Conasauga River near Conasauga, Polk Co., Tennessee). Holotype Alabama Mus. Nat. Hist. 83; specimens designated as paratypes UMMZ 51301 though from Conasauga River, Campbells Mill, Murray Co., Georgia.

amphichaenus Frierson, *Unio* (*Lampsilis*): 1898, *Nautilus*, 11: 109, pl. 1 (Sabine River, Logansport [De Soto Parish], Louisiana). Holotype USNM 159935; paratype UMMZ 107936.

andrewsii Marsh, *Quadrula*: 1902, *Nautilus*, 15: 115 (Holston River, Tennessee); 1902, *Nautilus*, 16: 8, pl. 1, upper two figs. as *andrewsae*. Figured holotype ANSP 83170.

archeri Frierson, *Quadrula*: 1905, *Nautilus*, 19: 13, pl. 1, figs. 1, 2 (Tallapoosa River, Tallassee [Elmore Co.], Alabama). Holotype UMMZ 113583.

aroanus H.B. Baker, *Anodontites*: 1930, *Occas. Pap. Mus. Zool., Univ. Mich.*, (210): 69, pls. 32, 33, fig. d (Cano Minapam, a tributary of Río Aroa, near Palma Sola, Venezuela). Holotype UMMZ 112619.

askewi Marsh, *Unio*: 1896, *Nautilus,* 10: 91, pl. 1, figs. 3,4 (Village Creek, Hardin Co.; Sabine River; *both* Texas). Figured holotype ANSP 70448a from the latter locality.

avellana Simpson, *Pleurobema*: 1900, *Proc. Acad. nat. Sci. Philad.,* 52: 81, pl. 2, figs. 6, 7 (Cahawba River, Alabama). Figured holotype UMMZ 79653.

beauchampii Marsh, *Quadrula*: 1902, *Nautilus,* 16: 7, pl. 1, lower two figs. (Little Tennessee River; Holston River; *both* Tennessee). Figured holotype ANSP 83169 from the former locality.

birgei F.C. Baker, *Anodontoides*: 1923, *Nautilus,* 35: 123 ([Lake Michigan] Sturgeon Bay, west of bridge, Door. Co., Wisconsin). Measured holotype UMMZ 209188, figured by Baker, 1928, *Bull. Wisc. geol. nat. Hist. Surv.,* (70), pt. 2: 180, pl. 68, figs. 1-2.

blatchleyi Daniels, *Lampsilis*: 1902, *Nautilus,* 16: 13, pl. 2 (Wabash River, Section 32, Linn Township, Posey Co., Indiana). Figured holotype UMMZ 82960 from the Indiana State Museum.

breviculus Call, *Unio*: 1887, *Proc. U.S. natl. Mus.,* 10: 499, pl. 28 (Currant River, Shannon Co., Missouri, and in Jacks Fork and Big Creek, tributaries to it). Lectotype MCZ 5020 selected by Johnson, 1975a, *Occas. Pap. Moll.,* 4: 141, specimen portrayed by Call in figs. 1, 1a, 1b from Jacks Fork, Shannon Co.; figured allotype MCZ 5023, figs. 2, 2a, 2b, from Big Creek [Fork, Texas Co.]; paralectotype UMMZ 240058 from MCZ 5021, Jacks Fork.

brimleyi S. Hart Wright, *Unio*: 1897, *Nautilus,* 10: 138 ([Walnut Creek of] Neuse River, Raleigh, [Wake Co.] North Carolina). Lectotype USNM 149651, selected by Johnson, 1967, *Occas. Pap. Moll.,* 3: 5, pl. 5, fig. 1, and the locality restricted to Walnut Creek; paralectotype UMMZ 22504.

brooksiana van der Schalie, *Anodonta*: 1938, *Ann. Carnegie Mus.,* 27, pl. 16 (Spout Pond Arm, Ferryland District, Southern Shore, Newfoundland). Holotype Carnegie Mus. 61.13137; paratypes in UMMZ, but not located.

bullocki F.C. Baker, *Quadrula quadrula*: 1928, *Bull. Wisc. geol. nat. Hist. Surv.,* (70), pt. 2: 87, pl. 46, figs. 1-3 (Fox River, near De Pere [Brown Co.], Wisconsin). Holotype UMMZ 209203.

burkei Walker, *Quincuncina*: 1922, *Nautilus,* 36: 3, pl. 1, figs. 1, 4 (Sikes Creek, a tributary of the Choctawhatchee River, Barbour Co., Alabama; also numerous other localities). Holotype UMMZ 94495.

chadwicki F.C. Baker, *Lampsilis siliquoidea*: 1928, *Bull. Wisc. geol. nat. Hist. Surv.,* (70), pt. 2: 279, pl. 91, figs. 5-8 (Lake Winnebago, Doemel Point, near Oshkosh [Winnebago Co.], Wisconsin). Lectotype UMMZ 209200 selected by Franzen, 1957, *Nautilus,* 71: 33, portrayed by Baker on pl. 91, figs. 5-6.

chipolaensis Walker, *Unio*: 1905, *Nautilus,* 18: 135, pl. 9, figs. 6, 7 (Chipola River, Florida). Figured holotype UMMZ 96363. The type locality was restricted to: Chipola River, 1 mi N of Marianna, Jackson Co., Florida, by Clench & Turner, 1956, *Bull. Fla. State Mus.,* 1: 176.

choctawensis Athearn, *Viliosa*: 1964, *Nautilus,* 77: 137, pl. 9, figs. c, d, e, f (Choctawhatchee River, 2 mi SW Carryville; about 1 mi downstream from U.S. Highway 90, Holmes Co., Florida). Holotype National Museum of Canada, Ottawa, 20096; paratype UMMZ 239360 from MCZ 249413.

cicatricoides Frierson, *Unio*: 1911, *Nautilus,* 25: 53, pl. 2, upper fig. (no locality [Wabash River, Indiana]). Holotype UMMZ 87570.

compertus Frierson, *Unio*: 1911, *Nautilus,* 25: 53, pl. 3, middle and lower figs. (Clinch and Holston rivers [Tennessee]). Lectotype UMMZ 87769, lower fig. selected by Johnson, 1972, *Occas. Pap. Moll.,* 3: 142, pl. 24, fig. 1.

crebristrata Anthony, *Monocondylaea*: 1865, *Am. J. Conchol.,* 1: 205, pl. 18, fig. 1 (Pegu, British Burmah). Holotype MCZ 47749; paratypes UMMZ 239358 from MCZ 178935.

cromwellii Lea, *Unio*: 1865, *Proc. Acad. nat. Sci. Philad.,* 17: 89 (Kiokee Creek, near Albany, Dougherty Co., Georgia); 1868, *J. Acad. nat. Sci. Philad.,* ser. 2, 6: 258, pl. 31, fig. 73; 1869, *Observ. genus* Unio, 12: 18, pl. 31, fig. 73. Figured holotype USNM 85280; possible paratype UMMZ 15777 from J. Lewis, who was not mentioned in the original description.

croninae Walker, *Nodularia*: 1922, *Nautilus,* 35: 5, pl. 1, figs. 2-3 (Zambesi River, Mongu Sealu, Barotze Valley, North Rhodesia). Holotype UMMZ 59694.

cuatotolapamensis H.B. Baker, *Elliptio (Sphenonaias) liebmanni*: 1922, *Occas. Pap. Mus. Zool., Univ. Mich.,* (106): 13, pl. 1, figs. 6, 7, pl. 3, fig. 22, pl. 4, figs. 20-25 (Río San Juan, Southern Vera Cruz, Mexico). Holotype UMMZ 31904, figured on pl. 4, fig. 22.

curtisii Frierson & Utterback, *Truncilla*: 1916, *Am. midl. Nat.,* 4: 453, pl. 6, fig. 14a-d, pl. 28, fig. 109A-D (White River, Hollister [Taney Co.], Missouri). Lectotype UMMZ 90748 from the White River, Forsyth, Taney Co., Missouri, selected by Johnson, 1978, *Bull. Mus. comp. Zool.,* 148: 272, pl. 13, fig. 10; paralectotype UMMZ 90748, pl. 13, fig. 7.

dakota Frierson, *Anodonta*: 1910, *Nautilus,* 23: 113, pl. 10 (Clear Lake, Ulvers Point, Deuel Co., South Dakota). Holotype UMMZ 87582.

detectus Frierson, *Unio*: 1911, *Nautilus,* 25: 52, pl. 2, lower fig., pl. 3, upper fig. (no locality [Ohio River]). Holotype UMMZ 87571.

elvae Walker, *Nephronaias*: 1924, *Nautilus,* 38: 52, pl. 1, figs. 1, 2 (Wanks River or Río Coco, Nicaragua). Known only from the figured holotype retained by W.H. Fluck [lost].

escambia Clench & Turner, *Fusconaia*: 1956, *Bull. Fla. State Mus.*, 1: 152, pl. 7, figs. 3, 4 (Escambia River, 3 mi SE Century, Escambia Co., Florida). Holotype MCZ 191470; paratype UMMZ 239361 from MCZ 191935.

ferrissii Marsh, *Unio*: 1891, *Nautilus,* 5: 30 (a small creek near Pilatka [Palatka, Putnam Co.], Florida). Type figured by Simpson, 1892, *Proc. U.S. natl. Mus.*, 15: 423, pl. 66, figs. 1-2, probably returned to Marsh [lost].

fictum Frierson, *Pleurobema*: 1927, *Check list N. Am. naiades,* p 43 (Cahaba River, Alabama). Holotype UMMZ 87575, figured by Frierson, 1928, *Nautilus,* 41: 139, pl. 3, fig. 2, 2a.

fimbriata Frierson, *Lampsilis*: 1907, *Nautilus,* 21: 86, pl. 12, two upper figs. and lower left one (Valles River [near Valles, San Luis Potosi State, Mexico]). Holotype UMMZ 87579.

flexuosa Simpson, *Quadrula*: 1900, *Proc. Acad. nat. Sci. Philad.*, 52: 83, pl. 2, fig. 8 (Holston River, Tennessee). Type in the Frierson collection, UMMZ [not located]. Frierson (1927, *Check list N. Am. naiades,* p 57) mentioned that the type of this species was in his collection and that it was merely an old shell of *Quadrula pilaris* Lea.

flucki Walker, *Anodontites*: 1924, *Nautilus,* 38: 53, pl. 1, figs. 3, 4 (Wanks River or Río Coco, Nicaragua). Figured type Walker collection 74610 [not located]; paratypes MCZ 167989 from Fluck.

flucki Bartsch, *Nephronaias*: 1906, *Proc. U.S. natl. Mus.*, 30: 393, pl. 27, figs. 2, 3; pl. 28, figs. 2, 3; pl. 29, figs. 1, 3 (Wounta River, NW of Kukallya, Nicaragua). Holotype USNM 106121; paratype UMMZ 239357 from MCZ 167986.

forsheyi Lea, *Unio*: 1859, *Proc. Acad. nat. Sci. Philad.*, 11: 155 ([Colorado River] Fayette Co., Texas; Alabama [Texas], Anthony); 1860, *J. Acad. nat. Sci. Philad.*, ser. 2, 4: 357, pl. 60, fig. 182; 1860, *Observ. genus* Unio, 8: 39, pl. 60, fig. 182. Figured holotype USNM 84169, labeled "Texas, Anthony"; paratype UMMZ 167845, from Anthony from MCZ.

fusca F.C. Baker, *Utterbackia imbecillis*: 1927, *Am. midl. Nat.*, 10: 222 ([Lake Michigan] Sturgeon Bay, Door Co., Wisconsin). Holotype UMMZ 209141 figured by Baker, 1928, *Bull. Wisc. geol. nat. Hist. Surv.*, (70), pt. 2: 175, pl. 103, fig. 14.

generosus Gould, *Unio*: 1847, *Proc. Boston Soc. nat. Hist.*, 2: 220 (Newville, [province of] Tavoy [Burma]). Holotype MCZ 169449 figured by Johnson, 1964, *Bull. U.S. natl. Mus.*, (239): 82, pl. 33, fig. 1; paratype UMMZ 239353 from MCZ 169450.

hagleri Frierson, *Unio* (*Pleurobema*): 1906, *Nautilus,* 13: 109, pl. 2 (north River, near Tynes [=Tyner, Tuscaloosa Co.], Alabama). Lectotype ANSP 77902a, two lower figs, selected by Johnson, 1972, *Occas. Pap. Moll.*, 3: 144, pl. 25, fig. 1; paralectotypes UMMZ 80804.

harciotti Frierson, *Elliptio*: 1927, *Check list N. Am. naiades,* p 38 (Guatemala). Holotype UMMZ 97047, figured by Frierson, 1928, *Nautilus,* 41: 139, pl. 3, fig. 4.

infossus H.B. Baker, *Anodontites*: 1930, *Occas. Pap. Mus. Zool., Univ. Mich.*, (210): 67, pl. 22, fig. e; pl. 23, fig. e (Cano Minapam, a tributary of Río Aroa, near Palma Sola, Venezuela). Holotype UMMZ 112621 portrayed in both figures.

iridella Pilsbry & Frierson, *Lampsilis*: 1907, *Nautilus,* 21, pl. 12, two lower right figs.; 1908, *Nautilus,* 22: 81 ([Valles River] Valles [San Luis Potosi State], Mexico). Holotype ANSP 93810a; paratypes UMMZ [not located].

jacksonianus Frierson, *Unio* (*Obovaria*): 1912, *Nautilus,* 26: 23, pl. 3, figs. 1-3 (Pearl River, Mississippi, and also Yalabusha River, Mississippi). Lectotype ANSP 106063a, figs. 1, 2, selected by Johnson, 1972, *Occas. Pap. Moll.*, 3: 145, pl. 26, fig. 4; paralectotypes UMMZ 107523.

jonesi van der Schalie, *Lampsilis*: 1934, *Nautilus,* 47: 125, pl. 15, figs. 1a, 1b, 2, 3a, 3b (Pea River, Prestons Mill, Dale Co., Alabama). Lectotype Alabama Mus. nat. Hist., portrayed on pl. 15, figs. 1a, 1b, selected by Johnson, 1967, *Breviora,* (270): 13; paralectotypes in UMMZ, not located.

kamerunensis Walker, *Spatha*: 1910, *Nautilus,* 24: 38, pl. 3, figs. 1-2 (Kribi River, 17 mi from Efulen, Kamerun). Figured holotype UMMZ 111952.

lacustris F.C. Baker, *Lampsilis gracilis*: 1922, *Nautilus,* 35: 131 (Lake Butte des Morts, off Plummers Point [Winnebago Co.], Wisconsin). Holotype UMMZ 209186, figured by Baker, 1928, *Bull. Wisc. geol. nat. Hist. Surv.*, (70), pt. 2: 237, pl. 80, figs. 5-6.

lacustris F.C. Baker, *Truncilla truncata*: 1928, *Bull. Wisc. geol. nat. Hist. Surv.*, (70), pt. 2: 227, pl. 28, figs. 1-2 (Lake Winnebago, Long Point Island [Winnebago Co.], Wisconsin). Holotype UMMZ 209214.

langi Pilsbry & Bequaert, *Mutela*: 1927, *Bull. Am. Mus. nat. Hist.*, 53: 432, pl. 39, figs. 3, 3a-b (Zambi, in the bed of an arm of the Congo [Republic of the Congo]). Holotype ANSP 133860a; paratypes UMMZ 239354 from MCZ 41068. "Is a synonym of *Mutela nilotica angustata* Sowerby" (*teste* Bequaert).

lewisi Walker, *Truncilla*: 1910, *Nautilus,* 24: 42, pl. 3, fig. 3, female; figs. 4, 5, male (Holston River,

Tennessee). Lectotype UMMZ 91456 selected by Johnson, 1978, *Bull. Mus. comp. Zool.*, 148: 283, pl. 15, fig. 8; paralectotype, pl. 15, fig. 6.

lobensis Frierson, *Parreysia*: 1913, *Nautilus*, 27: 85, pl. 5, lower figs. (Lobo River, Kamerun [Cameroon]). Holotype MCZ 21164; paratype UMMZ [not located].

magnalacustris F. C. Baker, *Alasmidonta calceolus*: 1928, *Bull. Wisc. geol. nat. Hist. Surv.*, (70), pt. 2: 188, pl. 72, figs. 12-16 ([Lake Michigan] Sturgeon Bay, Door Co., Wisconsin). Holotype UMMZ 209215; paratype UMMZ 209216.

marshalli Frierson, *Pleurobema*: 1927, *Check list N. Am. naiades*, p 43 (Tombigbee River, Boligee [Greene Co.], Alabama). Holotype UMMZ 80859 figured by Frierson, 1928, *Nautilus*, 41: 139, pl. 3, fig. 3.

mcglameriae van der Schalie, *Medionidus*: 1939, *Occas. Pap. Mus. Zool., Univ. Mich.*, (407): 1, pl. 1 (Tombigbee River, Epes, Sumpter Co., Alabama). Holotype UMMZ 130460.

mcmichaeli Clench & Turner, *Elliptio*: 1956, *Bull. Fla. State Mus.*, 1: 170, pl. 7, figs. 1-2 (Choctawhatchee River, 8 mi W Miller Cross Roads, Holmes Co., Florida, on Florida State Route 2). Holotype MCZ 191922; paratype UMMZ 239359 from MCZ 191827.

mcneili Anthony, *Anodon*: 1866, *Am. J. Conchol.*, 2: 144, pl. 6, fig. 1 ([Sand Lake] Michigan). Holotype MCZ 150644; paratype UMMZ 57099.

missouriensis Marsh, *Pleurobema*: 1901, *Nautilus*, 15: 74 (Black River, near Poplar Bluff, Butler Co., Missouri). Holotype UMMZ 38855 figured by Walker, 1915, *Nautilus*, 28: 140, pl. 5, figs. 1-2; also a smaller paratype.

moquinianus Dupuy, *Unio*: 1843, *Moll. Terr. et Fluv. Dépt. de Gers* [Auch et Paris], p 80, pl. (l'Arros; l'Echez à Vic de-Bigorre [Gers]). Figured syntypes in the Toulouse Mus.; two syntypes UMMZ 28229 from the latter locality.

nuda F. C. Baker, *Lasmigona costata*: 1928, *Bull. Wisc. geol. nat. Hist. Surv.*, (70), pt. 2: 145, pl. 59, figs. 3-6, text fig. 224 (Red Cedar River, W of Chetek, Barron Co., Wisconsin). Holotype UMMZ 209131 portrayed on pl. 59, fig. 3.

ortmanni Walker, *Micromya*: 1925, *Occas. Pap. Mus. Zool., Univ. Mich.*, (163): 1, pl. 1, figs. 1-6 (Green River, Mammoth Cave [Edmonson Co.]; also Sulphur Fork of Russell Creek, Adair Co.; *both* Kentucky). Holotype MCZ 167705; allotype MCZ 167702; both from the former locality.

ortmanni Frierson, *Unio* (*Nephronaias*): 1913, *Nautilus*, 27: 14, pl. 2 (Conchins River, near Quirigua [Izabal State], Guatemala, Atlantic drainage). Lectotype ANSP 117544a, upper figs. selected by Johnson, 1972, *Occas. Pap. Moll.*, 3: 146, pl. 30, fig. 3; paralectotypes UMMZ 108005.

ovatus Frierson, *Strophitus undulatus*: 1927, *Check list N. Am. naiades*, p 22 (Middle West). Lectotype UMMZ 87584 from Lyon Creek, Edwards Co., Illinois, selected by Johnson, 1972, *Occas. Pap. Moll.*, 3: 147, pl. 22, fig. 2; paralectotype UMMZ 87585.

ozarkensis Call, *Unio*: 1887, *Proc. U.S. natl. Mus.*, 10: 498, pl. 27 (Currant River, Shannon Co., Missouri, and in Jacks Fork and Big Creek tributaries to it). Lectotype MCZ 5707, selected by Johnson, 1975a, *Occas. Pap. Moll.*, 4: 143, male specimen portrayed in figs. 1-3; figured allotype MCZ 5705, fig. 4; paralectotypes UMMZ 54091, 92298 and 92299 *all* from Jacks Fork.

peggyae Johnson, *Anodonta*: 1965, *Breviora*, (213): 1-7, pl. 2, figs. 1-3 (SE shore of Lake Talquin [formed by a dam on the Ochlockonee River], Leon County public fishing ground, Leon Co., Florida). Holotype MCZ 251040, fig. 1; paratype UMMZ 239355 from MCZ 191840.

peguensis Anthony, *Unio*: 1865, *Am. J. Conchol.*, 1: 351, pl. 25, fig. 2 (Pegu, British Burmah). Holotype MCZ 161875; paratype UMMZ 239362 from MCZ 161874.

pepinensis F. C. Baker, *Lampsilis siliquoidea*: 1927, *Am. midl. Nat.*, 10: 223 (Lake Pepin, near Lake City [Wabasha Co.], Minnesota). Lectotype UMMZ 209208 selected by Franzen, 1957, *Nautilus*, 71: 34, figured by Baker, 1928, *Bull. Wisc. geol. nat. Hist. Surv.*, (70), pt. 2: 275, pl. 90, figs. 2-3.

pepinensis F. C. Baker, *Lasmigona costata*: 1928, *Bull. Wisc. geol. nat. Hist. Surv.*, (70), pt. 2: 144, pl. 59, figs. 1-2 (Lake Pepin, Lake City [Wabasha Co.], Minnesota). Holotype UMMZ 209133, portrayed on pl. 59, fig. 1.

pepinensis F. C. Baker, *Strophitus rugosus*: 1928, *Bull. Wisc. geol. nat. Hist. Surv.*, (70), pt. 2: 204, pl. 74, fig. 8 (Lake Pepin, near Lake City [Wabasha Co.], Minnesota). Holotype UMMZ 209137.

perglobosa F. C. Baker, *Lampsilis ventricosa*: 1928, *Bull. Wisc. geol. nat. Hist. Surv.*, (70), pt. 2: 285, pl. 93, figs. 1-4 (Lake Pepin, near Lake City, Wabasha Co., Minnesota). Holotype UMMZ 209195 portrayed on pl. 93, figs. 3-4.

pilsbryana Frierson, *Lampsilis*: 1927, *Check list N. Am. naiades*, p 83. Based on a specimen of *Unio purpuriatus* Frierson, *non* Say, figured by Frierson, 1912, *Nautilus*, 26: 22, pl. 3, figs. 4, 5 (no locality [Mexico]). Holotype UMMZ 91175.

pilsbryi Marsh, *Unio*: 1891, *Nautilus*, 5: 1 (Little Red River, Arkansas). Holotype ANSP 41589a figured by Pilsbry, 1892, *Proc. Acad. nat. Sci. Philad.*, 44: 131, pl. 8, figs. 7-8, and in 1892, *Nautilus*, 6, pl. 1, figs. 7-8; paratypes UMMZ 42931.

pleasii Marsh, *Unio*: 1891, *Nautilus,* 5: 2 (Little Red River, Arkansas). Lectotype ANSP 56480a selected by Johnson & Baker, 1973, *Proc. Acad. nat. Sci. Philad.,* 125: 166, pl. 9, fig. 5; allotype ANSP 56480; paralectotypes UMMZ 237354.

rafinesqueana Frierson, *Lampsilis*: 1927, *Check list N. Am. naiades,* p 69 ([Mud Creek] Moodys [10 mi N Tahlequah, Cherokee Co.], Oklahoma). Holotype UMMZ 87576 figured by Frierson, 1928, *Nautilus,* 41: 138, pl. 1, figs. 1, 2.

rubidula Frierson, *Quadrula*: 1905, *Nautilus,* 19: 14, pl. 1, figs. 3, 4 (Mulberry River, also Black Warrior River and North River [Tyner, Tuscaloosa Co.], Alabama). Holotype UMMZ 113535.

ruthveni H.B. Baker, *Lampsilis*: 1922, *Occas. Pap. Mus. Zool., Univ. Mich.,* (106): 29, pl. 11, fig. 53; pl. 12, fig. 53; pl. 13, figs. 51-54 (Río San Juan, near Hacienda de Cuatotolapam, Southern Vera Cruz, Mexico). Holotype UMMZ 34891 figured on pl. 13, fig. 51.

sajensis Frierson, *Elliptio*: 1927, *Check list N. Am. naiades,* p 37 (Saja River [4 mi W], Esmaralda, Guatemala). Holotype UMMZ 108010 figured by Frierson, 1928, *Nautilus,* 41: 139, pl. 2, fig. 2.

sampsoniana Frierson, *Quadrula flava*: 1927, *Check list N. Am. naiades,* p 55 (Elk River [McDonald Co.], Missouri). Lectotype UMMZ 92226 selected by Johnson, 1972, *Occas. Pap. Moll.,* 3: 149, pl. 25, fig. 5.

sanjuanensis H.B. Baker, *Lampsilis rovirosi*: 1922, *Occas. Pap. Mus. Zool., Univ. Mich.,* (106): 27, pl. 8, figs. 39-42 (Río San Juan, near Hacienda de Cuatotolapam, Southern Vera Cruz, Mexico). Holotype UMMZ 34890 figured on pl. 8, fig. 40.

selecta Wheeler, *Fusconaia*: 1914, *Nautilus,* 28: 76, pl. 4 (Cashe River, Nemo, Craighead Co., Arkansas). The measured and figured type was retained by Wheeler and is now thought to be in the Alabama Mus. nat. Hist.; paratypes UMMZ 38300.

semirasa Pilsbry, *Lampsilis*: 1910, *Proc. Acad. nat. Sci. Philad.,* 61: 534, pl. 26, figs. 7-9 (Ganima River, 3 mi SW Dieguito; Valles River, Mecos [*both* State of San Luis Potosi, Mexico]). Lectotype ANSP 99542a, fig. 7, from the former locality, selected by Johnson & Baker, 1973, *Proc. Acad. nat. Sci. Philad.,* 125: 170; paralectotypes UMMZ 39172 from the former locality.

simpsonianus Walker, *Medionidus*: 1905, *Nautilus,* 18: 136, pl. 9, figs. 4, 5 ([Ochlockonee River] Calvary [Grady Co.], Georgia). Holotype UMMZ 98510.

singleyanus Marsh, *Unio*: 1891, *Nautilus,* 5: 29 (small creek near Pilatka [Palatka, Putnam Co.], Florida). Holotype UMMZ 17628 figured by Simpson, 1892, *Proc. U.S. natl. Mus.,* 15: 426, pl. 68, figs. 4, 5, from the Frierson collection.

streckeri Frierson, *Lampsilis*: 1927, *Check list N. Am. naiades,* p 74 (Little Red River, Arkansas). Holotype UMMZ 91075 figured by Frierson, 1928, *Nautilus,* 41: 139, pl. 2, fig. 1.

subgibbosa Anthony, *Anodon*: 1866, *Am. J. Conchol.,* 2: 144, pl. 6, fig. 2 (Black Lake [near Holland, Ottawa Co.], Michigan). Holotype MCZ 161854; specimen identified by Anthony from White Lake, Muskegon Co., Michigan, UMMZ 165605.

subinflata Anthony, *Anodon*: 1865, *Am. J. Conchol.,* 1: 160, pl. 15, fig. 1 ([Shears Lake, Kent Co.] Michigan). Holotype MCZ 161854; paratypes UMMZ 165607 and 178936.

superiorensis Marsh, *Unio*: 1897, *Nautilus,* 10: 103, pl. 1, figs. 1, 2, 5 (Michipicoton River, upper shore of Lake Superior [Canada]). Figured holotype ANSP 70449a; paratype ANSP 70449, fig. 5; paratypes UMMZ 209139.

tennesseensis Frierson, *Strophitus undulatus*: 1927, *Check list N. Am. naiades,* p 22 (headwaters of the Tennessee River). Lectotype MCZ 16690 from Duck River, Shelbyville, Bedford Co., Tennessee, selected by Johnson, 1956, *Bull. Mus. comp. Zool.,* 115: 138, pl. 2, fig. 1; paralectotype UMMZ 87583 from Elk River, Tennessee.

tenuisculus Frierson, *Unio*: 1911, *Nautilus,* 25: 29, pl. 1, figs. 4-6 (Reedy Lake, Polk Co., Florida, in the Gulf drainage). Lectotype UMMZ 96312, figs. 4, 6, selected by Johnson, 1972, *Occas. Pap. Moll.,* 3: 150, pl. 29, fig. 3.

upsoni Marsh, *Unio*: 1880, "Read before the Mercer County, Illinois, Scientific and Historical Society, March 2, 1880. Mr. Marsh had copies of the description published and thinks that the species was described on the records. It was not figured." Simpson, 1900, *Proc. U.S. natl. Mus.,* 22: 539; Marsh, 1887, *Conchol. Exch.* [*Nautilus*], 1: 51 (Kishacaukee River, Winnebago County, Illinois). Not found in the UMMZ; syntype MCZ 5551 in the R.E. Call collection.

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ACKNOWLEDGEMENTS

Thanks are extended to Drs. H. van der Schalie and J.B. Burch who, over a period of many years, have always made the collection under their charge available. Thanks are also extended to Dr. C.M. Patterson, formerly in charge of the Museum of Zoology's mollusk collections, and to Mr. Robert W. Hanley, curatorial assistant, the former for the loan of material and the latter for answering numerous requests for information. Expenses incurred in travel necessary to prepare this paper were generously paid by the William F. Milton Fund, Harvard University.

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RICHARD I. JOHNSON

Museum of Comparative Zoology
Harvard University
Cambridge, Massachusetts 02138, U.S.A.

Malacological Review, 1979, 12: 37-40

PUNCTAL CANALS IN THE SHELL OF *MUSCULIUM SECURIS* (BIVALVIA: PISIDIIDAE)

J. Leonard Robertson and C. C. Coney

ABSTRACT

The punctal canals in the shells of *Musculium securis* were examined by scanning electron microscopy. These punctae tunnel through the complex crossed-lamellar layer but not through the outer periostracum layer. This was observed in both mature and larval clams. The outer epithelium of the mantle folds into each punctum and forms a tube lining the entire length of the canal. Speculative comments on the function of the punctum are presented.

INTRODUCTION

Microscopic examination of the shell of *Musculium securis* (Prime) has indicated the presence of tiny canals called punctae. Earlier investigators, using light microscopy, described these punctae in various Pisidiidae and speculated on their functions (see Schröder, 1907; Rosso, 1954). The purpose of this investigation was to observe these punctae and their associated mantle membrane interactions utilizing a scanning electron microscope (SEM).

MATERIALS AND METHODS

The *Musculium securis* used in this study were collected at Bays Mountain Lake, Kingsport, Sullivan Co., Tennessee. Voucher specimens have been deposited in the Museum of Zoology, The University of Michigan. The animals were prepared for SEM observation using standard techniques. Steel needles were inserted between the valves to force them open. The live clams were then fixed for five minutes in cold 4% osmium tetroxide. Water was removed from the tissues through an acetone series, and drying was accomplished in a Parr critical point drying apparatus. The specimens were then carefully dissected, exposing the inner surface of the shell and the delicate mantle tissues.

The shells were attached to aluminum stubs with DAG 154 graphite solution (Pelco). A 200 Å thick layer of gold was then plated onto the specimens in a Denton vacuum evaporator. Observations and photomicrographs were made using an ETEC scanning electron microscope.

RESULTS

The interaction of mantle and shell in the region of the punctae was observed in various ways. Upon complete removal of the mantle, the openings (ostia) of the punctae on the inner surface of the shell appeared as slight depressions (Fig. 1). When a portion of the mantle was left intact, only the outer layer of the epithelium was observed to be convoluted into the funnel-shaped ostia of the punctae (Figs. 2, 3). Magnification of the mantle tissues at x6000 revealed a multicellular composition of the outer epithelium in the region where it convoluted into the ostia (Fig. 4). At no point was the inner epithelial membrane of the mantle in contact with, or depressed into, the ostia of the punctae.

Observations of cross sections of the cracked shell showed that the punctae tunneled through the complex crossed-lamellar layer but did not enter the thin periostracum layer (Mackie, 1978). Tube-shaped projections of the outer mantle membrane were observed to go through the entire length of the punctae (Figs. 5, 6). Examination of prodissoconch larval shells and extramarsupial larval shells (Mackie & Huggins, 1976) showed that, just as in the adults, the punctae did not totally penetrate the shell. In no instances were large pyramidal cells observed to protrude completely through the larval shells. Punctae were not observed to penetrate through the periostracum layer of the larval or the adult shells.

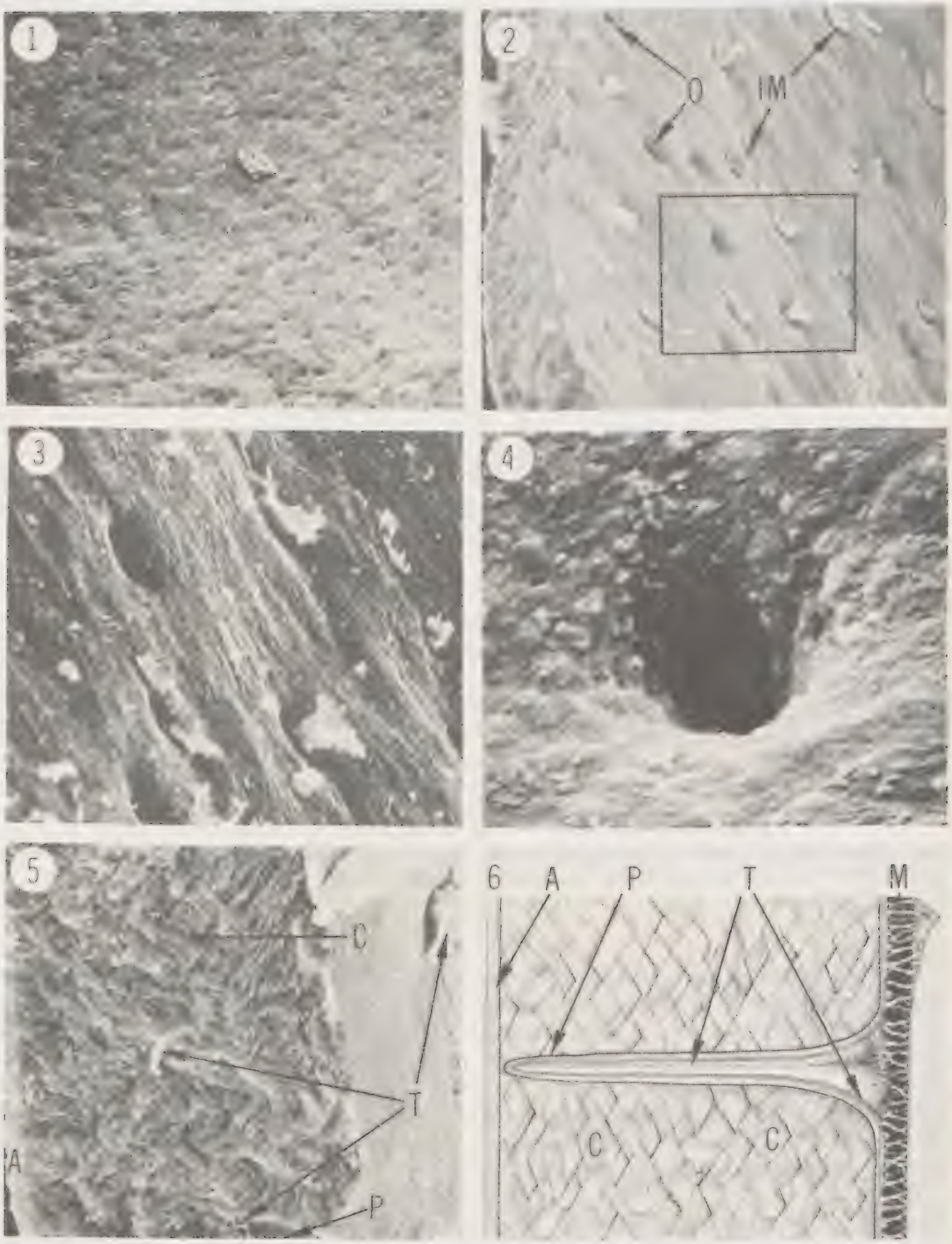

FIG. 1. Punctae openings (ostia) on the inner surface of the shell. Approximate magnification: x120. FIG. 2. Inner surface of a broken shell. O, ostia of punctae; IM, inner membrane of mantle. Approximate magnification: x400. FIG. 3. Enlarged view of the inset area in Fig. 2. Approximate magnification: x1000. FIG. 4. Multicellular outer membrane of the mantle folding into the ostium of a punctum. Approximate magnification: x6000. FIG. 5. Broken edge and inner surface of a shell. A, periostracum; C, complex crossed-lamellar layer; M, mantle; P, punctum; T, inner epithelium of mantle going into and through punctae, tube-shaped inside punctum. Approximate magnification: x1000. FIG. 6. Drawing of a shell and cross section of the mantle in the region of a punctum. See legend to Fig. 5 for key to labels.

DISCUSSION

Schröder (1907) earlier studied the shell structure and mantle epithelium of a congener, viz., *Musculium lacustre* (Müller). Using light microscopy, he observed the mantle epithelium to contain "large, flat polygonal cells" and "pyramidal cells with irregular bases." He further observed long processes from the pyramidal cells that "extended through the shell canals and ended at the periostracum." The present SEM study of *M. securis* showed a hollow, tube-shaped projection of outer mantle epithelium tissue protruding into and through the punctae canals (Fig. 6). The tube was multicellular in composition, not just a single process from a large pyramidal cell. In observing the larval forms of *M. transversum* (Say), Rosso (1954) assumed that the pyramidal cell processes protruded completely through the shells. The present study showed that the punctae did not penetrate the shell of either the adult of the developing young. The differences in the information presented by Schröder, Rosso and the present study could have been due to species differences (*M. lacustre, M. transversum* and *M. securis,* respectively) or to the higher resolution of the SEM.

The function of the punctae was not immediately obvious even when observed with the SEM. This situation led the present authors to the speculation that these punctae might be vestigial remnants of some previously functional structure that has been largely lost in evolution. Rosso (1954) assumed that the punctae have contemporary functional significance and presented a concise review of these functions as suggested by other investigators. With the additional information provided by this study, we identify at least four potential contemporary functions from those suggested by previous investigators: embryonic nourishment, secretory function, sensory function, and absorptive or respiratory function.

If the mantle tube in the punctum could be shown to penetrate the periostracum in a larval clam (see Rosso, 1954), the assumption that the punctum has an embryonic nourishment function would be supported. The present study, however, indicated just the opposite; punctae were not observed to penetrate the periostracum layer in the larval shells. For this reason, the present authors have considered embryonic nourishment as only a remotely possible function.

The tube shape of the mantle epithelium in the punctum has led us to favor the speculation that a secretory or sensory function is valid. The very presence of a tube suggests that something goes into or out of it. The punctum might be an apparatus through which mantle cells could secrete calcium compounds, nitrogenous waste compounds, carbon dioxide, or other substances. Rosso (1954) suggested the possibility that the function of the punctum was similar to that of the Haversian canals in bone. However, the open circulatory system of the clam would necessitate an alteration of the Haversian model since no capillaries were observed in conjunction with the punctum. The present study, and that of Mackie (1978), have shown the periostracum to be a dense layer. It must be pervious to any substance that the punctum would secrete or excrete outside the shell. It is therefore possible that the function of the punctum is to move some substance out of the clam through the shell. This could be especially of physiological importance when the valves are closed for prolonged periods.

It is equally as plausible to speculate that substances diffuse into the clam from the outside, as it is to speculate that they diffuse out through the punctae. These clams reportedly do not have high oxygen requirements (Thomas, 1965). They frequently have been found in low oxygen environments, such as the mud in the bottom of a pond, under ice in a pond that has been unaerated all winter, or in the mud of a temporarily dry stream or woods pond. If trans-periostracum oxygen diffusion is possible, it is a reasonable speculation that respiration is a function of the punctae, especially during those periods of stress just mentioned.

Another possible function could be that of monitoring the moisture content of the immediate environment around the clam. Although *Musculium securis* does not require a habitat

which dries up during part of the year, as does *Sphaerium occidentale* (Lewis) (Herrington, 1962), it may well be able to temporarily withstand a moderately desiccated environment by tightly closing the valves during such periods of stress. The moisture content of the sediments of a drying habitat could be monitored by the entrapped clam should the periostracum be partially permeable to water molecules. When the habitat refilled with water and the moisture content in the sediments increased, detection of change in the habitat status by the closed clam via methods discussed here might be possible. A mechanism involving simple water osmosis through the periostracum into the punctae could be possible. Further research will be necessary to determine the exact function of these unique canals.

ACKNOWLEDGEMENTS

We are indebted to Dr. J.B. Burch of The University of Michigan for his comments and gracious loan of museum specimens. We wish to thank Dr. G.L. Mackie of the University of Guelph for providing taxonomic confirmation of our tentative identifications. Additionally, we gratefully acknowledge Mr. Ran Coney for contributing the illustration in Fig. 6.

This work was supported in part by a grant from the Southern Regional Education Board.

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J. LEONARD ROBERTSON
C.C. CONEY

Department of Biological Sciences
East Tennessee State University
Johnson City, Tennessee 37601, U.S.A.

Malacological Review, 1979, 12: 41-49

THE SYSTEMATIC RELATIONSHIPS OF THE HYDROBIOID SNAIL GENUS *NYMPHOPHILUS* TAYLOR 1966 AND THE STATUS OF THE SUBFAMILY NYMPHOPHILINAE

Fred G. Thompson

ABSTRACT

Nymphophilus is a genus of hydrobioid snails endemic to the Cuatro Cienegas Basin of northern Mexico. Aspects of its internal anatomy demonstrate that *Nymphophilus* is closely related to other genera in North America and Europe. The oldest family-group taxon name available for this assemblage of genera is Nymphophili-(nae) Taylor 1966, which predates Orientalii-(dae) Radoman 1973. The taxonomic level (family, subfamily, tribe) assigned to this group cannot be determined until more is learned about the anatomy of other hydrobioid groups.

Nymphophilus is a monotypic genus endemic to the Cuatro Cienegas Basin of Coahuila, Mexico. Taylor (1966: 199) proposed the subfamily Nymphophilinae and included *Nymphophilus* as the only genus in the subfamily. Thus, the Nymphophilinae was considered endemic to the Cuatro Cienegas Basin.

The purpose of this paper is to demonstrate the systematic relationships of *Nymphophilus* to other hydrobioid genera and to determine the phylogenetic status of the subfamily Nymphophilinae, a member of the "Hydrobiidae." Taylor (1966: 199-203) provided a detailed description of the external morphology and the male reproductive system of this unusual snail. Critical information relating to trophic organs, the central nervous system, and the female reproductive system were not included in his account, and some aspects of the shell and the male reproductive system require additional observations. The material upon which this study is based was collected by the author from 4 localities in the Cuatro Cienegas Basin, Coahuila, Mexico, in March, 1964 (see below, Material Examined).

Examination of the soft anatomy of *Nymphophilus minkleyi* Taylor 1966 demonstrates that *Nymphophilus* is closely related to several genera of hydrobioids from eastern North America and is not distinguishable from them at the suprageneric level. Furthermore, *Nymphophilus* is not distinguishable at the suprageneric level from some European hydrobioids.

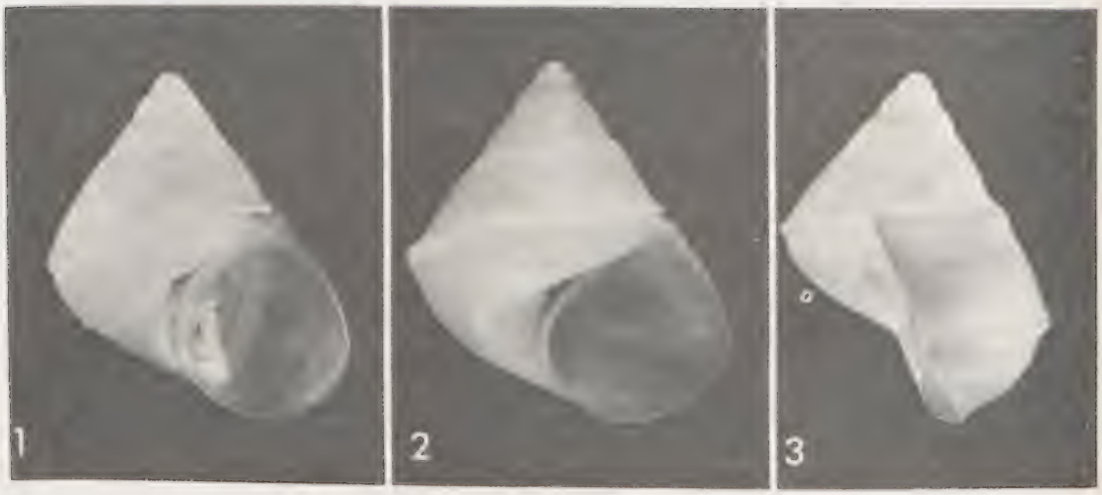
MATERIAL EXAMINED

Coahuila, Cuatro Cienegas Basin: Laguna Churince, 16 km SSW Cuatro Cienegas (UF 22626 - catalogue number, Florida State Museum); Poza de la Becerra, 14 km SW Cuatro Cienegas (UF 22630); spring 10 km SSW Cuatro Cienegas (UF 22628 - shells and anatomical specimens); spring creek 10 km SSW Cuatro Cienegas (UF 22625, 22627 - shells and anatomical specimens). All dissections and radular mounts were made from UF 22627.

NYMPHOPHILUS MINKLEYI TAYLOR

Nymphophilus minkleyi Taylor 1966, *Veliger*, 9: 199-203, pl. 13, figs. 15, 17, text-figs. 17-21.

Shell. The shell (Figs. 1-3) is trochiform with a rounded base and is about 0.72-0.87 times as wide as high. The spire is straight-sided and weakly concave in outline. The base is narrowly umbilicate with the perforation being half covered by the reflected columellar lip. The periphery is marked by a strong spiral keel that overlies a corresponding groove on the inside of the shell and lies just above the suture so that the keel tends to cause the whorls to be



FIGS. 1-3. *Nymphophilus minkleyi* Taylor (UF 22629)

slightly scalariform. The keel is continuous to the peristome in young specimens (Figs. 2,3), but in mature adults it usually fades about 1/4 of a whorl behind the peristome (Fig. 1). The suture is shallow but distinctly incised. There are about 5.1-5.6 whorls at maturity. The embryonic whorl is about 0.30 mm in diameter, perpendicular to the initial suture, and is sculptured with numerous minute anastomosing pits and wrinkles that are observable only with a scanning electron microscope (Figs. 4-7). The wrinkles are most strongly developed around the initial suture and are diminished elsewhere on the embryonic shell. The post embryonic whorls are sculptured with relatively coarse incremental striations that are crowded and continuous over the surface of the body whorl, but are irregular in intensity giving the surface a satiny sheen under high magnification. The peristome is complete across the parietal wall at maturity. The aperture is ovate in outline, being 0.83-0.95 times as wide as high. The posterior corner forms an obtuse angle. The aperture is about 0.47-0.60 times the height of the shell and in lateral profile lies at an angle of about 16-20° to the axis of the shell (Fig. 3). The outer lip and basal lip are thin and sharp. The columellar lip is considerably thickened and forms a heavy callus across the parietal wall at maturity.

Measurements based on 10 adults (UF 22629) selected to show maximum variation are: length, 7.0-9.0 mm; width, 5.7-7.0 mm; aperture height, 4.0-4.8 mm; aperture width, 3.5-4.2 mm.

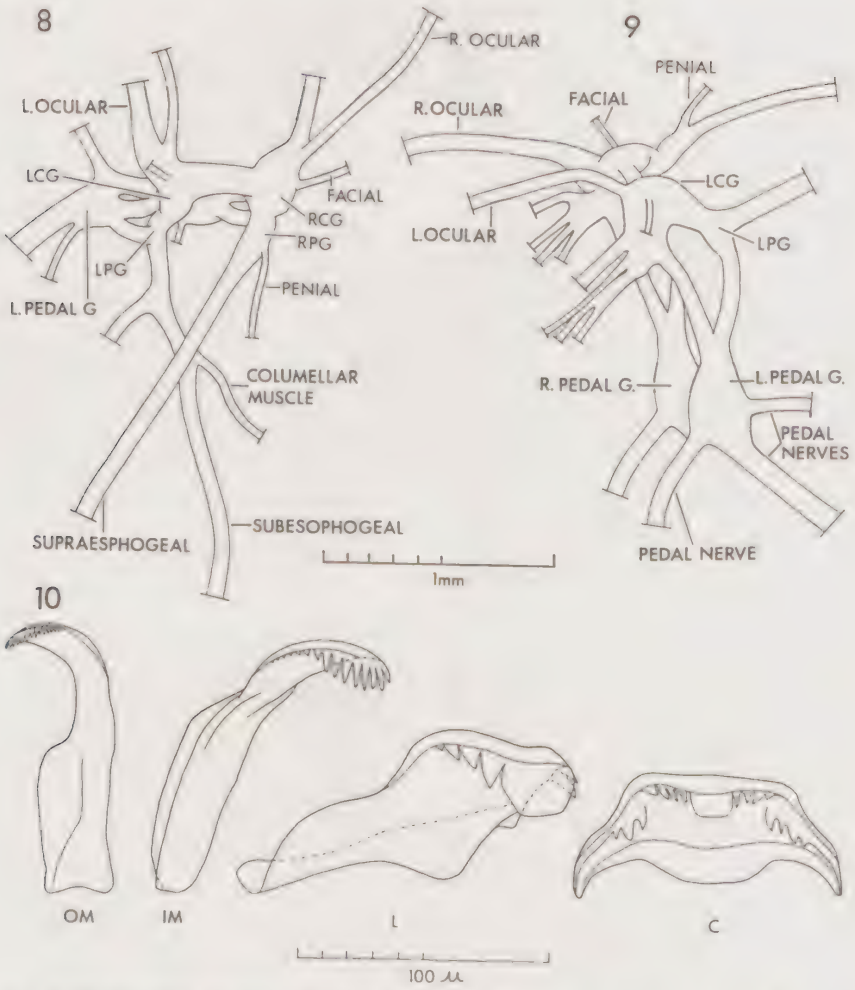
The operculum is broadly ovate, subspiral and consists of about 6 whorls. The nucleus is subcentral in position and lies below and to the left of the center. The outer surface is densely sculptured with coarse incremental striations.

Trophic organs. Twelve female radulae were examined from UF 22627. The radula (Fig. 10) is taenioglossid, and in most essential features, including the shape of the teeth, is like that of *Notogillia, Spilochlamys, Cincinnatia, Rhapinema* and *Marstonia* (see Thompson, 1968: 99-147; 1969: 142-160). The radula consists of 55-57 transverse rows of teeth with the cusp formula: $C\ \frac{(3\text{-}5)\text{-}1\text{-}(3\text{-}5)}{(2\text{-}4)\text{-}1\text{-}(2\text{-}4)}$, L (1-2)-1-2(3-4), IM (11-17), OM (11-15). The central tooth is about 100-105 μ wide and bears a large blunt-edged mesocone, 3-5 acuminate ectocones and 2-4 basocones on each side. The lateral tooth is hatchet-shaped. The rasping margin, like the central tooth, bears a large blunt-edged mesocone, which is bordered by 1-2 acuminate entocones and 3-4 acuminate ectocones. The inner marginal tooth bears about 11-17 slender lanceolate cusps. The outer marginal has about 11-15 similar but smaller cusps.

FIGS. 4-7. *Nymphophilus minkleyi* Taylor (UF 22629). SEM micrographs of the embryonic sculpture of the initial whorl of 3 specimens (Figs. 4 and 5 are of the same specimen). Fig. 4, x337; Fig. 5, x345; Fig. 6, x348; Fig. 7, x336.

The radular teeth are highly asymmetrical in the number of cusps on each side of the mesocone of the central tooth and the number of cusps on corresponding opposite laterals and marginals.

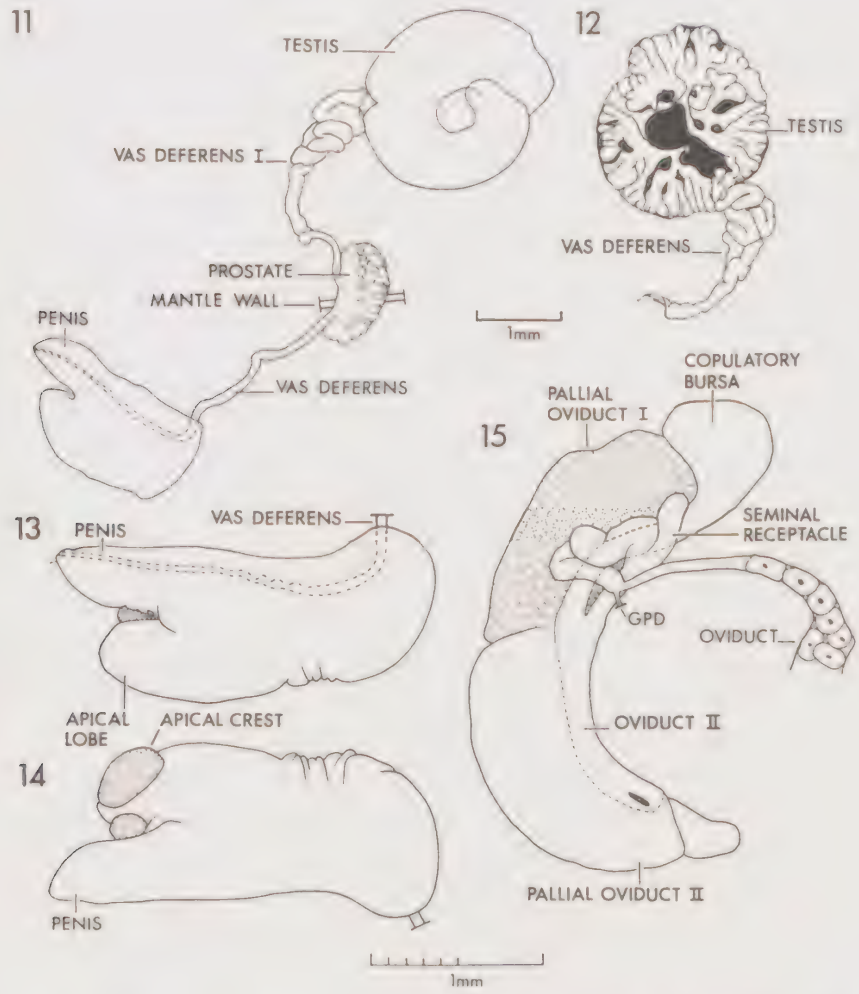
The salivary glands lie dorso-lateral to the buccal mass and are separate throughout their lengths. The distal end of each gland is slightly contorted posterior to the buccal mass. The glands extend posteriorly to the base of the optic tentacles and just anterior to the brain.



FIGS. 8-10. *Nymphophilus minkleyi* Taylor. FIGS. 8, 9. Dorsal and lateral views of the brain. LCG = left cerebral ganglion; LPG = left pleural ganglion; RCG = right cerebral ganglion; RPG = right pleural ganglion. FIG. 10. Radular teeth. OM = outer marginal; IM = inner marginal; L = lateral; C = central.

Nervous System. Six specimens were examined for this system. The central nervous system of *Nymphophilus* (Figs. 8,9) is similar to that described by Radoman (1973) for the Orientaliidae. Essential features to be noted are: (1) the optic nerves form a slight ganglial swelling near their base; (2) the pleural ganglia are juxtaposed to the cerebral ganglia; (3) the pedal nerves are reduced to 3 principal nerves arising from the pedal ganglia; (4) the pleuro-supraintestinal connective is long; (5) the supraintestinal ganglion lies along the left side of the coelom; (6) the pleuro-subesophageal connective is very short; (7) the subesophageal ganglion lies below the esophagus and is doubled; (8) the penis is inervated by the right pleural ganglion.

Female Reproductive System. Fourteen specimens were dissected. The pallial oviduct is 2-segmented (Fig. 15). The anterior pallial oviduct lies along the columellar margin of the mantle cavity and terminates anteriorly just posterior to the mantle collar. The posterior pallial oviduct is separated from its anterior counterpart at the posterior margin of the mantle cavity. The oviduct-I is thin-walled and is enlarged just below the ovary. In all specimens that I dissected, the oviduct-I contained about 4-7 primary oocytes that were about 300 μ long. The oviduct-I passes along the ventral floor of the coelom to the posterior margin of



FIGS. 11-15. *Nymphophilus minkleyi* Taylor. FIG. 11. Male reproductive system. FIG. 12. Ventral view of testis. FIG. 13. Dorsal view of verge. FIG. 14. Ventral view of verge. FIG. 15. Mesad view of female reproductive system exclusive of the gonad. The upper scale is for Figs. 11, 12 and 15; the lower scale is for Figs. 13 and 14.

the mantle cavity at which point a short gonopericardial duct (GPD) connects it with the pericardial cavity. The oviduct forms a posteriorly directed double-looped convolution along the mesad surface of the posterior pallial oviduct. The seminal receptacle is small, simple, and papilliform and enters the oviduct at the end of the loop. (The seminal receptacle is equivalent to the seminal receptacle-2 of Radoman, 1973.) The bursa copulatrix is very large and sacculate and lies completely beyond the posterior end of the posterior pallial oviduct. The bursal duct is about as long as the posterior pallial oviduct and enters the oviduct-II at the junction with the anterior pallial oviduct. The bursal duct lies impressed into, but is not covered by, the mesad surface of the posterior pallial oviduct. The female genital opening of the oviduct-II enters the mantle cavity. An omniphoric groove is absent as is also a suprapedal fold.

Male Reproductive System. Four specimens were dissected. Many other males were examined externally. The male reproductive system is described in detail by Taylor (1966). Only salient points are mentioned here (Figs. 11-14). The verge originates on the right side

of the nape within the mantle cavity and is bilobed terminally, forming a penis and an apical lobe (see Thompson, 1968, 1969, 1977, for comparisons with other North American genera). The penis lies along the right terminal margin of the verge. It is relatively stout compared to most allied American genera and extends beyond the apical lobe. The apical lobe bears 1 or 2 globular apocrine glands on the mesad surface. The testis is multilobed and extends nearly completely throughout the digestive gland along its dorsal surface. The vas deferens-I is enlarged and convoluted immediately below the testis and becomes reduced in size just above the prostate. The prostate lies along the columellar margin and partially overlaps the mantle cavity. There is no connective between the vas deferens and the mantle cavity. The vas deferens-II continues anteriorly from the ventral margin of the prostate along the right mantle wall and enters the nape just posterior to the mantle collar. The vas deferens-II forms a low diagonal ridge on the nape between the right mantle wall and the verge. The vas deferens-II is only slightly convoluted within the verge and discharges at the tip of the penis.

DIAGNOSIS OF *NYMPHOPHILUS*

Nymphophilus minkleyi has a remarkably distinctive shell compared to most other hydrobine snails. It is less distinctive anatomically. It is characterized by the following combination of characters. Shell: 1) conico-trochiform with a strong peripheral keel that overlays a corresponding peripheral groove on the inside of the shell; 2) peristome incomplete, connected across the parietal wall with a callus; 3) shell large, about 7-9 mm long; 4) umbilicus very narrowly rimate; 5) embryonic shell sculptured with minute anastomosing pits and wrinkles that are most strongly developed along the initial suture; 6) postembryonic sculpture consisting of strong incremental striations; 7) operculum subspiral, consisting of about 6 whorls; Radula: 8) C $\frac{(3\text{-}5)\text{-}1\text{-}(3\text{-}5)}{(2\text{-}4)\ \text{-}\ (2\text{-}4)}$, L (1-2)-1-(3-4), IM (11-17), OM (11-15); 9) mesocone of central and lateral teeth enlarged with squarish or bluntly rounded scraping margins; 10) central tooth with 2-4 basocones on each side; Female: 11) bursa copulatrix very large and sacculate, lying completely beyond the posterior end of the posterior pallial oviduct; Male: 12) verge bilobed, bearing 1-2 apocrine glands on the mesad surface of the apical lobe; remainder of verge lacking apocrine glands; 13) vas deferens forming a transverse ridge in body wall between prostate and verge.

The features outlined above characterize *Nymphophilus* as a distinct genus, but not as a higher taxonomic category. *Nymphophilus* differs anatomically from other North American and European genera only by degree of characters, not by qualitative factors. It is most similar to *Marstonia* on the basis of the reproductive systems. Both genera are alike in having few glands on the verge and in having a short penis that hardly extends beyond the end of the verge. Furthermore, the glands are confined to the apical lobe of the verge. *Rhapinema* has a similar pattern of glands, but it has a long slender penis that is about as long as the rest of the verge. Other genera have a short penis similar to *Marstonia* and *Nymphophilus*, but they have more numerous glands, which are more widely dispersed over the surface of the verge and the penis. The radula of *Nymphophilus* is unique among closely related genera in having 2-4 basocones on each side of the central tooth and in having gouge-shaped mesocones on the central and lateral teeth. Other genera have only a single basocone on each side and have acuminate mesocones. The embryonic sculpture of the shell and the peripheral keel with its underlying internal groove also are unique. Other closely related genera lack the enlarged wrinkled embryonic sculpture characteristic of *Nymphophilus*. Among related taxa, *"Pyrgulopsis" scalariformis* (Wolf) and *"P." letsoni* (Walker) have peripheral keels, but they lack corresponding underlying grooves internally.

OTHER BILOBED HYDROBIOID GENERA - THE NYMPHOPHILINAE

Nymphophilus shares many features with other North American and European genera. These characteristics indicate common phylogeny. The earliest family-group taxon name available for this assemblage of genera is Nymphophilinae Taylor 1966. Orientaliidae Radoman 1973 (with Orientaliinae) is the only other family-group taxon name applied to a genus of this group and it is a junior secondary synonym of Nymphophilinae. The systematics of the hydrobioid snails is unsettled to the extent that rigid applications of family and subfamily names is not possible. Nymphophilinae is used here primarily as a convenience in referring to this group of genera. Probably the group should be recognized only as a tribe. North American genera include: *Fontelicella* Gregg & Taylor 1965; *Birgella* Baker 1926; *Cincinnatia* Pilsbry 1891; *Marstonia* Baker 1926; *Notogillia* Pilsbry 1953; *Rhapinema* Thompson 1969; *Spilochlamys* Thompson 1968 (for anatomical data see Gregg & Taylor, 1965; Thompson, 1977). *Pyrgulopsis* Call & Pilsbry 1886 and *Orygoceras* Brusina 1882 may also belong in this group, but their soft anatomies are insufficiently known to substantiate this relationship (see Taylor, 1974, for notes on *Orygoceras*). European genera include: *Avenionia* Nicolas 1882 (see Boeters, 1970: 119); *Belgrandia* Bourguignat 1869 (see Giusti, 1970: 295-298; Giusti & Pezzoli, 1972: 202-208); *Litthabitella* Bole 1971 (see Boeters, 1974: 90-91); *Mercuria* Boeters 1971 (see Boeters, 1971: 177-180; Boeters, 1976: 95-98); *Microna* Clessin 1890 (see Boeters, 1970: 115-135); *Orientalia* Radoman 1972 (see Radoman, 1966: 247-249; Radoman, 1972: 196).

Radoman (1973: 6-11) places several other European genera in close relationship with *Orientalia* (and thus with this group) on the basis of the number and locations of seminal receptacles on the loop of oviduct-I, but he provides little additional data to support these proposed relationships. Davis, Kitikoon & Temcharoen (1976: 280-281) demonstrate that the reproductive system of hydrobioids is non-conservative in evolution and has undergone major changes among taxa radiating into new environments and geographic regions. Because of the high adaptability of the female reproductive system of hydrobioids in general, no major emphasis should be placed on the numbers and position of the seminal receptacles without additional supportive data. Thus, the relationships of the genera listed by Radoman (1973) require substantiation with additional data relating to the female reproductive system.

The only shell feature that distinguishes the Nymphophilinae lies in the embryonic microsculpture. For a comparison with *Cincinnatia, Marstonia, Notogillia, Nymphophilus* and *Spilochlamys*, see Thompson (1977). Basically the embryonic sculpture consists of anastomosing tubercles, wrinkles and pits. Minor modifications exist in particular genera, such as the enlarged step-like wrinkles that occur along the initial suture in *Nymphophilus* (Figs. 6,7). Otherwise, the sculpture is similar to that which is adjacent to the enlarged wrinkle in *Nymphophilus*. North American genera that I have examined belonging to other suprageneric groups have very different types of embryonic sculpture.

The nymphophid genera have in common the following anatomical traits: 1) the oviduct-I is connected to the pericardium via a gonopericardial duct; 2) the oviduct-I bears a single seminal receptacle, which is homologous to the seminal receptacle-2 of Radoman (1973); 3) the oviduct-II bears a single appendicular bursa copulatrix which lies in or along the side of the posterior pallial oviduct; 4) the transverse septum of the mantle cavity intersects near the middle of the pallial oviduct in the female and the prostate in the male; 5) the verge bears only a single duct, the vas deferens; 6) the verge is bilobed distally, bearing a terminal apical lobe and a laterally placed penis; 7) the surface of the verge bears various patterns of apocrine glands. These patterns are characteristic of the various genera listed above (*Birgella* lacks such glands, but I consider this significant only as a criterion of generic significance within this subfamily); 8) basocones are present on the central tooth of the radula; 9) the nervous system

is an epiathroid type with the features outlined earlier in this paper for *Nymphophilus* (I have examined the nervous systems only of *Cincinnatia, Marstonia* and *Nymphophilus*. Various authors have described the nervous system of European genera).

The genera discussed above are alike to the extent that generic diagnostic characteristics occur only in the shell, the operculum, the apocrine gland pattern on the verge and in the radula. Significant variations in the nervous system occur in the lengths of the connectives and commissures, but these are secondary variations that are a function of the size of the snail. They are only of value at the species level of taxonomy. Within this group small species have relatively shorter connectives and commissures than do larger species (Thompson & McCaleb, 1978).

Within the Nymphophilinae, the North American genera are most similar to each other in the patterns of apocrine glands on the verge. Likewise, the European genera are most similar to each other in this trait. North American genera usually have relatively enlarged glands on the apex of the apical lobe. European genera do not have such pronounced apical glands.

Considering the non-conservative evolutionary tendencies of hydrobioid reproductive systems, these genera are remarkably alike in the structure of the verge and its apocrine glands. A non-conservative system can diverge in its basic plan. Likewise, a non-conservative system can converge in some features. Because of the similarities demonstrated in the other anatomical structures and systems, it is apparent that these genera constitute a natural group (monophyletic) of closely related taxa, and the similarities of the male reproductive system are not a consequence of convergence from less related groups (polyphyletic).

The Nymphophilinae represent a well-defined group characteristic of the regions where it is found: North America and Europe. The group is disjunct in its present distribution, probably not as a consequence of dispersion but as a consequence of plate tectonics. The absence of this group in Asia argues against dispersion. The origin of this group would predate the separation of Laurasia into North America and Europe by the opening of the Atlantic Ocean, in which case the group probably originated in the Triassic or earlier.

ACKNOWLEDGEMENTS

The photographs constituting Figs. 1-3 were made by Donna Born Drake, Gainesville, Florida. The scanning electron microscope photographs in Figs. 2-7 were made by Sylvia Scudder, Technician II, Florida State Museum, on a Cambridge Mark II scanning electron microscope at the University of Florida. The other illustrations were rendered by Nancy Halliday, Staff Artist, Florida State Museum. These drawings were made with the aid of a camera lucida.

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FRED G. THOMPSON

Florida State Museum
University of Florida
Gainesville, Florida 32611, U.S.A.

Malacological Review, 1979, 12: 51-58

ALLOZYMES OF ETHIOPIAN *BULINUS SERICINUS* AND EGYPTIAN *BULINUS TRUNCATUS*[1]

K.-H. Wurzinger

ABSTRACT

Allozyme analysis via horizontal starch gel electrophoresis of three laboratory populations of *Bulinus sericinus* from Ethiopia and two laboratory populations of *B. truncatus* from Egypt indicates that the Ethiopian *B. sericinus* is only a local representative of the more widely distributed *B. truncatus*. The following enzymatic activities were analysed: acid phosphatase (two loci), alkaline phosphatase, non-specific esterases (eight loci), glutamate-oxaloacetate transaminase (two loci), alanine dehydrogenase, β-hydroxybutyrate dehydrogenase (two loci), malate dehydrogenase, malic enzyme, 6-phosphogluconate dehydrogenase, phosphohexoseisomerase, aldehyde oxidase, xanthine oxidase (two loci) and hemoglobin. The populations examined possessed identical alleles at 22 of the 28 loci examined, and shared common alleles at the remaining six loci.

INTRODUCTION

Bulinus sericinus (Jickeli), a member of the *truncatus* species group of the African planorbid subfamily Bulininae, has at various times been considered a distinct species (e.g., Mandahl-Barth, 1957; Wright & Brown, 1962), a subspecies of *B. truncatus* (Mandahl-Barth, 1960, 1965; Brown, 1965) or a synonym of *B. truncatus* (Brown & Wright, 1972). Most recently, Wu & Burch (1975) compared *B. sericinus* from its type locality (Toquor River at Merkerka, Eritrea, Ethiopia) to a population of *B. truncatus* from Egypt, and concluded that, due to the close similarity in shell and body morphology, esterase iso-enzymes and foot-muscle antigens, the Ethiopian species is probably only a race of *B. truncatus*.

The present work is a continuation of the study by Wu & Burch, and compares the allozymes of three populations of Ethiopian tetraploid snails and two populations of *Bulinus truncatus* from Egypt, using horizontal starch gel electrophoresis.

MATERIALS AND METHODS

The populations utilized in this study were all laboratory-bred stocks maintained at the Museum of Zoology, The University of Michigan (UMMZ). The snails were originally from the following localities.

Pop. 1 - *Bulinus truncatus*, Kafr-el-Sheik, Egypt
Pop. 2 - *Bulinus truncatus*, Iflaka Bilharzia Project Area, Behaira Province, Egypt
Pop. 3 - *Bulinus sericinus*, Toquor River at Merkerka, Ethiopia (type locality)
Pop. 4 - *Bulinus* sp., 205 km N of Addis Ababa, on Debra Birhan Road, Ethiopia
Pop. 5 - *Bulinus* sp., Lake Awasa, Sidamo Province, Ethiopia (albino)

Populations 2 and 3 are the same populations used by Wu (1972) and by Wu & Burch (1975).

The animals were maintained in glass aquaria and fed Tetra-Min^R fish food. Prior to the laboratory analyses, they were placed in plastic trays and starved for 48 hours to clear their digestive tracts. They were then frozen and stored at -90°C. Voucher specimens have been deposited in the UMMZ collections.

Sample preparation

Individual animals were subsequently thawed, checked as to whether they were phallic or aphallic and then crudely minced with a scalpel. The resulting slurry of each individual animal was placed into individual

[1] Supported by research grants from the Smithsonian Institution (Grant No. FC8-09483) and the National Institutes of Health (Public Law 480, Agreement No. 03-044-N).

1 ml Sorvall[R] centrifuge tubes with 2 volumes of a modified Manwell & Baker (1968) extraction buffer, which was composed of 10 mM Tris-buffer, containing 10 mM glycylglycine, 10 mM $CaCl_2$, 1% digitonin, 0.1 mM NAD and 0.1 mM NADP at pH 8.0. The samples were homogenized by sonication with a Bronwill Biosonic[R] III ultrasonic homogenizer equipped with a microprobe tip. Following sonication, the samples were centrifuged at 4°C in a Sorvall RC-2B refrigerated centrifuge equipped with a SS-34 rotor, at 16,000 rpm for 30 minutes. The resulting clear supernatant was stored at -70°C in 50 microliter aliquots until used for horizontal starch gel electrophoresis.

Starch gel electrophoresis

Horizontal starch gel electrophoresis was performed, using 12.5 g of electrostarch (lot 307) per 100 ml of gel buffer. The starch was mixed with the gel buffer in a side-arm filter flask and heated over a Bunsen burner with a medium hot flame as described by Smith (1968). The cooked starch gel solution was then degassed for 60 seconds with a water aspirator, poured into a plexiglass mold (14 x 14 x 1 cm) and covered with a glass plate. After cooling for one hour at room temperature (23-25°C), the gel was placed into a refrigerator (2-4°C) overnight.

The samples to be electrophoresed were applied to 9 x 5 mm pieces of Whatman 3 MM chromatography paper and inserted into a slot cut 3 cm from the cathodal end of the gel. Usually 16 to 20 samples were inserted per slab.

The loaded gel was placed horizontally over two buffer trays with platinum electrodes. Paper wicks (Handywipes[R]) were used to establish contact between the gel and the electrode buffer in the trays. The entire gel assembly was placed into a refrigerator at 0-2°C and connected to a constant voltage power supply (Heathkit model PS-4, IP-32 or IP-17).

Following electrophoresis, the gels were sliced horizontally into five 2 mm thick slices using a Buchler-type gel slicer, and stained for various enzymatic activities after a 30-minutes pre-incubation period in the staining buffer.

Starch gel electrophoresis buffers

Three different buffer systems were used to resolve the various enzymes. Buffer system I was the discontinuous buffer system of Poulik (1957). The gel buffer contained 76 mM Tris and 5 mM citric acid. The electrode buffer contained 0.3 M boric acid and 60 mM NaOH. Buffer system II was a continuous Tris-EDTA-borate system, at pH 8.6. The gel and electrode buffers were prepared by dilution from a stock solution containing 0.9 M Tris, 0.5 M boric acid, and 0.1 M EDTA (disodium salt). The gel buffer contained 40 ml of stock solution diluted to 1 liter. The electrode buffer contained 450 ml of stock solution diluted to 4 liters with distilled water. Buffer system III was the Tris-EDTA-maleate buffer system at pH 7.4 (Shaw & Prasad, 1970). The electrode buffer contained 0.1 M Tris, 0.1 M maleic acid, 10 mM EDTA and 10 mM $MgCl_2$. The pH was adjusted to 7.4 using NaOH. The gel buffer was a 1:10 dilution of the electrode buffer.

Electrophoresis was terminated after the bromphenol blue marker dye had migrated 9 cm from the origin. This took approximately six hours at 25 mA/gel for buffer system I, eight hours at 45 mA/gel for buffer system II and 18 hours at 30 mA/gel for buffer system III.

Enzyme assays

The assay solutions for detecting the various enzymatic activities were modified from Shaw & Prasad (1970), Selander et al. (1971), Ayala et al. (1972) or Coles (1969a,b).

Esterases (EST) (buffer system I). Four different substrates were used routinely. These were α-naphthyl acetate (αNA), β-naphthyl acetate (βNA), α-naphthyl propionate (αNP), and α-naphthyl butyrate (αNB). The staining solution contained 1 ml of substrate (1% w/v in acetone), 50 mg of Fast Blue RR salt in 50 ml of 0.2 M Tris-HCl, pH 7.4. Fast Blue BB salt was used with βNA, since it gave better localization of enzyme activity with this substrate than did the Fast Blue RR salt.

Acid phosphatase activity (AcP) (buffer system I or III). The gel slice was pre-incubated for one hour in 0.2 M acetate buffer, pH 5.0. The staining solution contained 50 mg of α-naphthyl acid phosphate (sodium salt), 50 mg of Fast Blue RR salt or 50 mg of Fast Black K salt in 50 ml of 0.2 M acetate buffer, pH 5.0.

Alkaline phosphatase (AlP) (buffer system I or III). The gel slice was pre-incubated for one hour in 0.2 M Tris-HCl, pH 9.0. The staining solution contained 50 mg of α-naphthyl acid phosphate, 30 mg of $MgCl_2$ and 50 mg of Fast Blue RR salt in 50 ml of 0.2 Tris-HCl, pH 9.0.

Glutamate-oxaloacetate transaminase (GOT) (buffer system I and III). The staining solution contained 100 mg of α-keto-glutaric acid, 150 mg of α-aspartic acid, 5 mg of pyridoxal-5-phosphate and 100 mg of Fast Blue BB salt in 50 ml of 0.2 M Tris-HCl, pH 8.0.

Aldehyde oxidase (AO) (buffer system II or III). The staining solution contained 1 ml of a saturated aqueous solution of benzaldehyde, 10 mg of MTT and 5 mg of PMS in 50 ml of 0.2 Tris-HCl, pH 8.0.

Xanthine oxidase (XO) (buffer system II or III). The staining solution contained 80 mg of hypoxanthine, 10 mg of MTT and 5 mg of PMS in 50 ml of 0.2 M Tris-HCl, pH 8.0. The hypoxanthine was first

dissolved in 1-2 ml of 1N NaOH, to which were added 48 ml of 0.2 M Tris-HCl, pH 7.4. The final pH of this solution was approximately 8.0.

α-glycerophosphate dehydrogenase (αGPDH) (buffer system I or II). The staining solution contained 100 mg of α-D,L-glycerophosphate, 20 mg of βNAD$^+$, 12 mg of MTT, 4 mg of PMS and 1 ml of 0.1 M $MgCl_2$ in 50 ml of 0.2 M Tris-HCl, pH 8.0.

Octanol dehydrogenase (ODH) (buffer system I or II). Three substrates were used. These were 95% ethanol; 0.2 ml of hexanol in 1 ml of 95% ethanol; or 0.2 ml of octanol in 1 ml of 95% ethanol. The staining solution contained 1 ml of substrate solution, 15 mg of βNAD$^+$, 10 mg of MTT and 5 mg of PMS in 50 ml of 0.2 M Tris-HCl, pH 8.0.

α-alanine dehydrogenase (AlaDH) (buffer system I). The staining solution contained 400 mg of α-alanine, 20 mg of βNAD$^+$, 10 mg of MTT and 3 mg of PMS in 50 ml of 0.2 M Tris-HCl, pH 8.0.

β-hydroxybutyrate dehydrogenase (βHBDH) (buffer system I). The staining solution contained 40 mg of β-hydroxybutyric acid (sodium salt), 10 mg of βNAD$^+$, 20 mg of MTT and 3 mg of PMS in 50 ml of 0.2 M Tris-HCl, pH 8.0.

Malate dehydrogenase (MDH) (buffer system I, II or III). The staining solution contained 5 ml of 2 M D,L-malic acid (pH 7.0), 10 mg of βNAD$^+$, 20 mg of MTT, 5 mg of PMS in 50 ml of 0.2 M Tris-HCl, pH 8.0.

Sorbitol dehydrogenase (SoDH) (buffer system II). The staining solution contained 500 mg sorbitol, 15 mg of βNAD$^+$, 15 mg of MTT and 3 mg of PMS in 50 ml of 0.2 M Tris-HCl, pH 8.0.

6-phosphogluconate dehydrogenase (6PGD) (buffer system II). The staining solution contained 30 mg of 6-phosphogluconic acid, 10 ml of 0.1 M $MgCl_2$, 10 mg of NADP$^+$, 20 mg of MTT, 4 mg of PMS in 40 ml of 0.2 M Tris-HCl, pH 8.0.

Malic enzyme (Me) (buffer system I or III). The staining solution contained 5 ml of 2 M malic acid (pH 7.0), 20 mg of NADP$^+$, 20 mg of MTT, 5 mg of PMS in 40 ml of 0.2 M Tris-HCl, pH 8.0.

Phosphoglucomutase (PGM) (buffer system II). The staining solution contained 165 mg of glucose-1-phosphate containing at least 1% of glucose-1-6-diphosphate, 10 ml of 0.1 M $MgCl_2$, 20 mg of MTT, 4 mg of PMS, 80 units of βNAD$^+$-glucose-6-phosphate dehydrogenase from *Leuconostoc mesenteroides* (Sigma No. G2383), 25 mg of βNAD$^+$ in 40 ml of 0.2 M Tris-HCl, pH 8.0.

Phosphohexose isomerase (PHI) (buffer system I or II). The staining solution contained 27 mg of fructose-6-phosphate, 10 ml of 0.1 M $MgCl_2$, 20 mg MTT, 5 mg PMS, 20 units of βNAD$^+$-glucose-6-phosphate dehydrogenase and 10 mg of βNAD$^+$ in 40 ml of 0.2 M Tris-HCl, pH 8.0.

Hemoglobin (Hb) (buffer system I, II or III). The staining solution contained 0.04% Coomassie Blue G-250 in 3.5% perchloric acid. This is a general protein stain. Hemoglobin was also visible on the unstained gels. However, staining with the protein stain made the bands more pronounced.

For each of the above enzymatic assays, gel slices incubated in the staining solutions without substrate served as controls. For the dehydrogenases, gel slices incubated with substrate but without βNAD$^+$ served as additional controls for oxidases.

Laboratory chemicals

The chemicals used in this investigation were of reagent grade or higher purity. Glucose-1-phosphate was purchased from Wessex Biochemicals, Bournemouth, England; MTT was obtained from Eastman Kodak Co., Rochester, New York, U.S.A.; all other chemicals and reagents for the enzyme assays were obtained from the Sigma Chemical Corp., St. Louis, Missouri, U.S.A. Electrostarch Lot 307 was obtained from the Electrostarch Co., Madison, Wisconsin, U.S.A.

Chromosome number determination

The chromosome number of the snails was determined using the acetic-orcein squash technique of LaCour (1941) on ovotestis (gonad) fixed in methanol:acetic acid (3:1) as described by Patterson & Burch (1978).

RESULTS

All of the populations used in this study had 36 pairs (n=36, 2n=72) of chromosomes, i.e., they were all tetraploid. Specimens of population 1 were all euphallic, whereas the other four populations were primarily aphallic (Table 1).

TABLE 1. Chromosome numbers and phallic characteristics of experimental snails.

Pop. No.	Locality	Chromosome No.	No. euphallic	No. aphallic	% aphallic
1	Egypt	n=36	55	0	0
2	Egypt	n=36	7	32	82
3	Ethiopia	n=36	4	20	83
4	Ethiopia	n=36	0	34	100
5	Ethiopia	n=36	0	90	100

Table 2 summarizes the results of the enzymatic analysis. Figs. 1 and 2 graphically illustrate a number of the enzymatic activities resolved in this study.

TABLE 2. Alleles at various enzyme loci in five populations of *Bulinus*.

Enzyme	Alleles				
	Pop. 1	Pop. 2	Pop. 3	Pop. 4	Pop. 5
AcP-1	1.00	0.92	0.92	1.00	1.00
AcP-2	1.00	1.00	1.00	1.00	1.00
AlP	1.00	1.00	1.00	1.00	1.00
EST-1	1.00	1.00	1.00	1.00	1.00
EST-2	1.00	1.00	1.00	1.00	1.00
EST-3	1.00	0.84	1.00	1.00	1.00
EST-4	1.13/1.40	1.13/1.40	1.00	1.00	1.00/1.13
EST-5	1.00	1.00	1.00	1.00	1.00
EST-6	1.00	1.00	1.00	1.00	1.00
EST-7	1.00	1.00	1.00	1.00	1.00
EST-8	1.00	1.00	1.00	1.00	1.00
GOT-1	1.00	1.00	1.00	1.00	1.00
GOT-2	1.00	1.00	1.00	1.00	1.00
AlaDH	1.00	1.00	1.00	1.00	1.00
αGPDH-1	1.00	0.93	1.00	1.00	1.00
αGPDH-2	1.00	0.93	1.00	1.00	1.00
βHBDH-1	1.00/1.10	1.00/1.10	1.00/1.10	1.00/1.10	1.00/1.10
βHBDH-2	1.00	1.00	1.00	1.00	1.00
MDH	1.00	1.00	1.00	1.00	1.00
ODH	1.00	1.00	1.00	1.00	1.00
SoDH	1.00	1.00	1.00	1.00	1.00
ME	1.00	1.00	1.00	1.00	1.00
6PGD	1.00	1.00	1.00	1.00	1.00
PGM	NS	NS	NS	NS	NS
PHI	1.00	1.00	1.00	1.00	1.00
AO	1.00	1.12/1.00	1.12/1.00	1.12/1.00	1.00
XO-1	1.07/1.00	1.07/1.00	1.07/1.00	1.07/1.00	1.07/1.00
XO-2	1.00	1.00	1.00	1.00	1.00
Hb	1.00	1.00	1.00	1.00	1.00

NS = activity detected but not scorable.

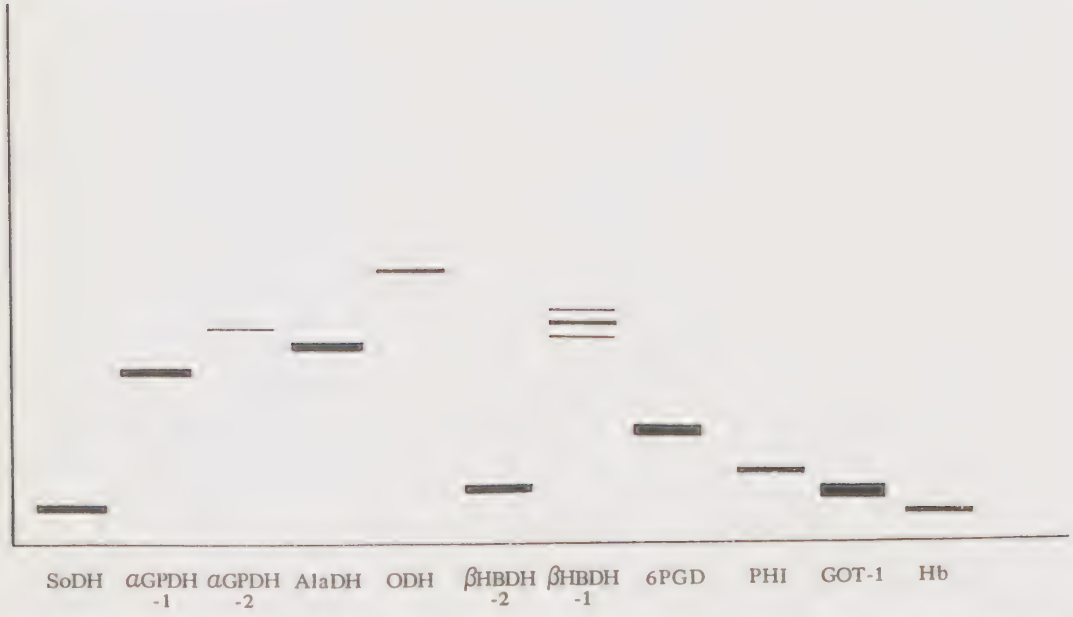

FIG. 1. Schematic diagram of allozyme patterns in individual *Bulinus truncatus* from Ethiopia and Egypt. Patterns shown are sorbitol dehydrogenase (SoDH), α-glycerophosphate dehydrogenase-1 (αGPDH-1), αGPDH-2, alanine dehydrogenase (AlaDH), octanol dehydrogenase (ODH), β-hydroxybutyrate dehydrogenase-2 (βHBDH-2), βHBDH-1 (1.00/1.10), 6-phosphogluconate dehydrogenase (6PGD), phosphohexose isomerase (PHI), glutamate oxaloacetate transaminase-1 (GOT-1) and hemoglobin (Hb). The numbers in parentheses are alleles found in the different populations (see Table 2).

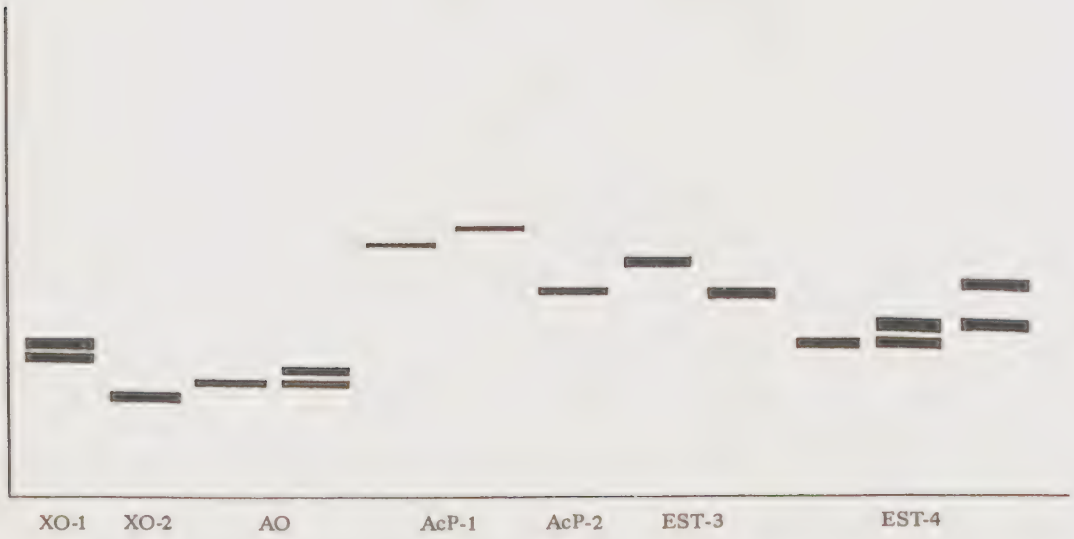

FIG. 2. Schematic diagram of allozyme patterns in individual *Bulinus truncatus* from Ethiopia and Egypt. Patterns shown are xanthine oxidase-1 (XO-1) (1.07/1.00), XO-2, aldehyde oxidase (AO) (1.00; 1.12/1.00), acid phosphatase-1 (AcP-1) (0.92; 1.00), AcP-2, esterase-3 (EST-3) (1.00; 0.84) and EST-4 (1.00; 1.13/1.00; 1.40/1.13). The numbers in parentheses are alleles found in the different populations (see Table 2).

A minimum of 20 individual animals from each population was utilized to determine the intrapopulation variation of each of the various enzymatic activities assayed. No intrapopulation variation was detected in any of the five populations sampled.

Population 5, which is an albino population, was designated as the reference population. Individual enzyme bands of that population were given a relative mobility designation of 1.00. In multibanded systems, the slowest band of the reference population was designated as the 1.00 band. The mobilities of the various electromorphs in all populations examined are presented as mobilities relative to the 1.00 band of the reference population, similar to the method of Hubby & Lewontin (1966). Independent zones of enzymatic activity are numbered sequentially from the most anodal to the most cathodal. Electromorphs are scored as autosomal loci with codominant alleles.

Esterases. Eight zones of non-specific esterase activity were recognized in the populations utilized in this study. In any one individual, up to 10 bands of esterase activity were detectable with αNA as the substrate. Most of the esterase bands were invariant, i.e., they were found in individuals of all of the populations; they will be described and characterized as to substrate and inhibitor specificity at a later date. The only variable esterases detected were EST-3 and EST-4. EST-3 is the major activity visualized with αNB. Populations 1, 3, 4 and 5 all possessed the same band, whereas population 2 possessed a different, slower band with a mobility of 0.84 relative to the fast band of the other populations. EST-4 is the major activity detected with βNA and Fast Blue BB salt. Four bands of activity were detected in the individuals examined. The individuals of populations 1 and 2 both possessed bands $4^{1.13}$ and $4^{1.40}$; the individuals of population 5 possessed bands $4^{1.00}$ and $4^{1.13}$.

Acid phosphatase (AcP). Two regions of acid phosphatase activity were detected. AcP-1 was a two-banded region; within any one population only one band was detected. Populations 2 and 3 were monomorphic for the slow band, which had a mobility of 0.92 relative to the fast band found in the individuals of populations 1, 4 and 5.

AcP-2 developed as a poorly defined band, of invariant mobility. No variation within or between populations was detected.

Alkaline phosphatase (AlP). One zone of non-specific alkaline phosphatase activity was detected. Satisfactory resolution of this enzymatic activity was not achieved with any of the buffers employed. Typically it developed as a 1 to 1.5 cm broad zone of variable intensity.

Glutamate oxaloacetate transaminase (GOT). Two monomorphic regions of GOT activity were detected in all individuals examined. GOT-1 migrated anodally in all three buffer systems. GOT-2 was only adequately resolved in buffer system III, where it migrated cathodally.

α-glycerophosphate dehydrogenase (αGPDH). Two weak bands of activity referable to this enzyme were detected in all individuals examined. Populations 1, 3, 4 and 5 all possessed the same bands, whereas population 2 was characterized by somewhat slower bands, which had a mobility of 0.93 relative to the fast bands. These enzymes are tentatively identified as monomorphic αGPDH-1 and αGPDH-2.

Malic enzyme (Me). A single broad zone of malate dehydrogenase activity was detected with $NADP^+$ as cofactor. This enzymatic activity migrated cathodally in buffer system III. No variation between populations was detected.

Malate dehydrogenase (MDH). Two broad zones of malate dehydrogenase activity were detected with βNAD^+ as cofactor. This enzymatic activity resolved poorly on all buffer systems examined. Although streaking was a major problem, no significant variation within or between populations was detected in the mobility of this enzyme. Addition of βNAD^+ to the gel and electrode buffers improved resolution somewhat. The slow zone of activity occupied the same position as did Me and thus may be that enzyme.

β-hydroxybutyrate dehydrogenase (βHBDH). Two regions of βHBDH activity were detected. The fast region, designated as βHBDH-1, consisted of a three-banded pattern interpreted as a diallelic system with heterodimer formation. All individuals examined in these

five populations appear to be fixed heterozygotes. The slow region, designated as βHBDH-2, consisted of a single, invariant band of activity. No inter- or intrapopulation variation was observed.

Octanol dehydrogenase (ODH). A single, monomorphic band was detected with all three substrates in all individuals examined. No intra- or interpopulation variation was detected. Greatest activity was obtained with octanol as substrate. Activity using ethanol was detected only after prolonged (12 hours) incubation.

Alanine dehydrogenase (AlaDH). A single, monomorphic band was detected in all individuals examined. No inter- or intrapopulation variation was detected.

Sorbitol dehydrogenase (SoDH). A single, slow, weak band of sorbitol dehydrogenase activity was detected in all individuals examined. No variation was found.

6-phosphogluconate dehydrogenase (6PGD). A single, invariant zone of activity was detected in all individuals examined.

Phosphoglucomutase (PGM). Although activity referable to this enzyme was detected in all individuals examined, the resolution was poor. Streaking rendered most samples uninterpretable.

Phosphohexose isomerase (PHI). A single, monomorphic band of activity referable to this enzyme was detected in all individuals examined. No variation within or between populations was observed.

Xanthine oxidase (XO). Two regions of XO activity were detected with hypoxanthine as substrate. XO-1, the fast region, consisted of two bands of activity, whereas XO-2, the slow region, consisted of a single, monomorphic band of activity. Addition of βNAD^+ to the staining solution did not result in the detection of any additional bands.

Aldehyde oxidase (AO). Two regions of activity were detected with benzaldehyde as substrate. The slow region occupied the same position as XO-2, and thus may be that enzyme. The fast region, designated as AO, was a variable enzymatic activity. Populations 1 and 5 contained only a single band of AO activity, whereas populations 2, 3 and 4 had an additional faster band. No variation was detected within populations.

Hemoglobin (Hb). A single invariant band referable to this protein was detected in all individuals examined.

DISCUSSION

The allozyme data reported here furnish substantial non-morphological evidence of the close genetic similarity of the Ethiopian *Bulinus sericinus* and the Egyptian *B. truncatus*. The Ethiopian and the Egyptian populations examined possessed identical alleles at 22 of the 28 presumptive genetic loci assayed and shared common alleles at the remaining six loci. Only esterase-4 had alleles unique for each of the geographic areas. The Egyptian populations were heterozygous for alleles 1.13 and 1.40, while two of the Ethiopian populations were homozygous for the 1.00 allele. The albino population was heterozygous for the 1.00 and 1.13 alleles. Both the Egyptian and the Ethiopian populations contained fixed heterozygotes for the EST-4, βHBDH-1, AO and XO-1 loci. These are easily explainable in terms of their tetraploidy. All five populations were very uniform in their genetic composition. No intrapopulation variation in any of the 28 presumptive genetic loci was observed. This lack of variation may largely be due to three different factors: 1) the individuals examined were all from populations that had been in laboratory culture for many generations and had experienced periodic populations crashes (bottleneck effect); 2) the laboratory populations had been founded by only one or a very few individuals (founder effect); and 3) the aphallic *Bulinus* populations must, out of necessity, self-fertilize. All three of these factors would tend to reduce variation within the populations and to promote homozygosity.

The present study strongly supports the conclusion of Wu & Burch (1975) and of Brown & Wright (1972) that *Bulinus sericinus* of Ethiopia is only a local form of *B. truncatus*. This

conclusion is based on the very close similarity in morphology (Brown & Wright, 1972; Wu & Burch, 1975), egg proteins (Brown & Wright, 1972), foot muscle esterases (Wu & Burch, 1975), chromosome number (Burch, 1969), susceptibility to infection with *Schistosoma haematobium* (Brown & Wright, 1972; Wu & Burch, 1974; Wurzinger, unpubl.), as well as the allozyme data presented in this study.

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K.-H. WURZINGER

Museum of Zoology and Division of Biological Sciences
The University of Michigan
Ann Arbor, Michigan 48109, U.S.A.

Malacological Review, 1979, 12: 59-65

A CYTOLOGICAL AND ELECTROPHORETIC COMPARISON OF JORDANIAN *BULINUS* WITH THREE OTHER TETRAPLOID *BULINUS* POPULATIONS[1]

K.-H. Wurzinger and E.K. Saliba

ABSTRACT

Bulinus truncatus from Jordan were compared to populations of *B. truncatus* from Syria, Egypt and Ethiopia, using allozymes resolved by horizontal starch gel electrophoresis. No differences in the four populations could be detected in 18 of the 22 presumptive loci analyzed. The Jordanian and Syrian populations differed from the other populations in acid phosphatase-2, esterase-3 and esterase-4. The Syrian population differed from the other three populations in acid phosphatase-1 and esterase-1. All four populations had 36 pairs (2n=72) of chromosomes, i.e., were tetraploid.

INTRODUCTION

Bulinus truncatus (Audouin), the molluscan intermediate host of *Schistosoma haematobium*, the causative agent of human urinary schistosomiasis, was not known from Jordan until Saliba et al. (1976) reported a focus from the Jordan Valley. Except for the Jordan River, which has not yet been surveyed because it constitutes a military zone, subsequent surveys failed to disclose any other foci in the valley.

Bulinus truncatus is widely distributed throughout the Middle East. It has been reported from all states immediately surrounding or close to Jordan. It occurs in Egypt, Syria, Lebanon, Iraq, Iran, Saudi Arabia (Wright, 1973), as well as in areas in Israel relatively close to the Jordan Valley (Lengy & Wolff, 1971). It is thus probable that the *Bulinus* found in Jordan were introduced from one of the surrounding areas.

The focus of *Bulinus truncatus* in Jordan has been eliminated. However, since there is a potential of reinvasion, it would be of interest to eventually determine, if possible, the specific area from which the *Bulinus* found in Jordan originated. With this in mind, horizontal starch gel electrophoresis was used to compare the *B. truncatus* from Jordan with three populations of the same species from Ethiopia, Egypt and Syria.

MATERIALS AND METHODS

The populations of *Bulinus truncatus* used in this investigation were as follows.

1. Egypt, Kafr-el-Sheik. Laboratory population, collected in November 1977 by Adly A. Michael.
2. Ethiopia, Lake Awasa, Sidamo Province. Laboratory population, collected March 1971 by C.T. Lo.
3. Jordan, Jordan Valley, Al-Masri area. Laboratory population, collected 1975/1976 by E.K. Saliba.
4. Syria, Raqqa area, in Euphrates Valley. Field population, collected by the staff of the Syrian Schistosomiasis Control Center, July 1978 (only snails not shedding trematode cercariae were used in this study).

The animals were maintained in glass aquaria and fed lettuce or Tetra-Min^{R} fish food. Prior to the laboratory analyses, they were placed into plastic trays and starved for 48 hours in order to clear their digestive tracts. They were then chilled on crushed ice, the bodies removed from the shell, and the gonads removed and fixed in modified Carnoy's fluid (3:1 ethyl alcohol:glacial acetic acid) for later chromosome number determination. The snails were checked as to whether they were phallic or aphallic. The field collected Syrian snails were also examined for infection by parasites. The whole snail body (minus gonad) was then prepared for starch gel electrophoresis. Voucher specimens have been deposited in the Museum of Zoology, The University of Michigan.

[1] Supported by research grants from the Smithsonian Institution (Grant No. FC8-09483) and the National Institutes of Health (Public Law 480, Agreement No. 03-044-N), and the University of Jordan.

The snails were crudely minced with a scalpel and the resulting slurry placed into individual 1 ml Sorvall[R] centrifuge tubes with an equal volume of a modified Manwell & Baker (1968) extraction buffer, which was composed of 10 mM Tris-buffer, containing 10 mM glycylglycine, 10 mM $CaCl_2$, 1% digitonin, 0.1 mM NAD and 0.1 mM NADP, pH 7.0. The samples were homogenized by sonication with a Bronwill Biosonic[R] III ultrasonic homogenizer equipped with a microprobe tip. The samples were centrifuged at 4°C in a Sorvall RC-2B refrigerated centrifuge equipped with a SS-34 rotor at 16,000 rpm for 30 minutes. The resulting clear supernatant was stored at -70°C in 50 microliter aliquots until used for horizontal starch gel electrophoresis. Eleven individuals of each of the four populations were examined.

Horizontal starch gel electrophoresis was performed as described by Smith (1968), using 12.5 g electrostarch/100 ml of buffer. The cooked and degassed starch was poured into a plexiglass mold (14 cm x 14 cm x 1 cm) and covered with a glass plate. The samples were applied to 9 x 5 mm pieces of Whatman 3 MM chromatography paper and inserted into a slot cut 3.0 cm from the cathodal end of the gel. Usually 16 to 20 samples were inserted per slab. Following electrophoresis, the gel was sliced horizontally into three or four slices using a Buchler-type gel slicer and stained for various enzymatic activities. The staining solutions were modified from Shaw & Prasad (1970).

Three different buffer systems were used to resolve the various enzymes. Buffer system I was the discontinuous buffer system of Poulik (1957). The gel buffer contained 76 mM Tris and 5 mM citric acid. The electrode buffer contained 0.3 M boric acid and 60 mM NaOH. Buffer system II was a continuous Tris-EDTA-borate system, at pH 8.6. The gel and electrode buffers were prepared by dilution from a stock solution containing 0.9 Tris, 0.5 M boric acid and 0.1 M EDTA (disodium). The gel buffer contained 40 ml of stock solution diluted to 1 liter. The electrode buffer contained 450 ml of stock solution diluted to 4 liters with distilled water. Buffer system III was the Tris-EDTA-maleate buffer system at pH 7.4 (Shaw & Prasad, 1970). The electrode buffer contained 0.1 M Tris, 0.1 M maleic acid, 10 mM EDTA and 10 mM $MgCl_2$. The pH was adjusted to 7.4 using NaOH. The gel buffer was a 10-fold dilution of the electrode buffer.

Electrophoresis was terminated after the bromophenol blue marker dye had migrated 9 cm from the origin. This took approximately six hours at 25 mA/gel for buffer system I, eight hours at 45 mA/gel for buffer system II and 18 hours at 30 mA/gel for buffer system III.

The starch used in this investigation was electrostarch lot 307, obtained from the Electrostarch Co., Madison, Wisconsin, U.S.A. All other chemicals were purchsed from the Sigma Chemical Corp., St. Louis, Missouri, U.S.A., and were of the highest purity available.

The chromosome number of the snails was determined on ovotestes using the aceto-orcein squash technique of LaCour (1941).

RESULTS

The individuals of all four populations examined had 36 pairs (2n=72) of chromosomes, and, except for one of the field collected Syrian snails, none of the snails used in this study were infected with parasites. The one infected snail harbored unidentified eye-spotted cercariae. All of the individuals of the Egyptian population were euphallic, whereas the other populations were primarily aphallic (Table 1).

Table 2 summarizes the data of the electrophoretic analysis. Figs. 1 and 2 graphically illustrate a number of the enzymatic activities resolved in this study.

The Ethiopian population, which is albino, was designated as the reference population. Individual enzyme bands of that population were assigned a relative mobility value of 1.00. In multibanded systems, the slowest band of the reference population was designated as the 1.00 band. The mobilities of the various electromorphs detected in the populations examined are presented as mobilities relative to the 1.00 band of the reference population. Independent zones of enzymatic activity were numbered sequentially from the most anodal to the most cathodal. Electromorphs are scored as autosomal loci with codominant alleles.

Esterases (EST) (buffer system I). Esterase activity was studied with α-naphthyl acetate (αNA), β-naphthyl acetate (βNA) and α-naphthyl butyrate (αNB) as substrates. Five of the eight zones of non-specific esterase activity detected were monomorphic, i.e., no differences were observed within or between the populations examined (Fig. 3). EST-2, EST-6 and EST-8 were weakly staining single bands of activity detected with all three substrates. EST-5 was poorly resolved by the systems employed. Where scorable, activity referable to this locus developed as two lightly staining bands of activity detected with αNB, but not the other two

TABLE 1. Chromosome numbers, phallic characteristics and number of infected animals in four populations of *Bulinus truncatus*.

Population	No. examined	Chromosome No.	No. euphallic	No. aphallic	% aphallic	No. infected
Ethiopia	11	n=36	0	11	100	0
Egypt	11	n=36	11	0	0	0
Jordan	11	n=36	0	11	100	0
Syria	11	n=36	3	8	73	1

TABLE 2. Alleles of various enzyme loci in four populations of *Bulinus truncatus*.

Enzyme	Alleles			
	Jordan	Syria	Egypt	Ethiopia
AcP-1	1.00	1.00/1.09	1.00	1.00
AcP-2	1.00/1.13	1.00/1.13	1.00	1.00
AlP	1.00	1.00	1.00	1.00
EST-1	1.00	1.04	1.00	1.00
EST-2	1.00	1.00	1.00	1.00
EST-3	0.84/1.00	0.84/1.00	1.00	1.00
EST-4	1.13	1.13	1.40/1.13	1.00/1.13
EST-6	1.00	1.00	1.00	1.00
EST-7	1.00	1.00	1.00	1.00
EST-8	1.00	1.00	1.00	1.00
GOT-1	1.00	1.00	1.00	1.00
GOT-2	1.00	1.00	1.00	1.00
αGPDH-1	1.00	1.00	1.00	1.00
αGPDH-2	1.00	1.00	1.00	1.00
βHBDH-1	1.10/1.00	1.10/1.00	1.10/1.00	1.10/1.00
βHBDH-2	1.00	1.00	1.00	1.00
MDH-1	1.00	1.00	1.00	1.00
MDH-2	1.00	1.00	1.00	1.00
AO	1.00	1.00	1.00	1.00
XO-1	1.07/1.00	1.07/1.00	1.07/1.00	1.07/1.00
XO-2	1.00	1.00	1.00	1.00
Hb	1.00	1.00	1.00	1.00

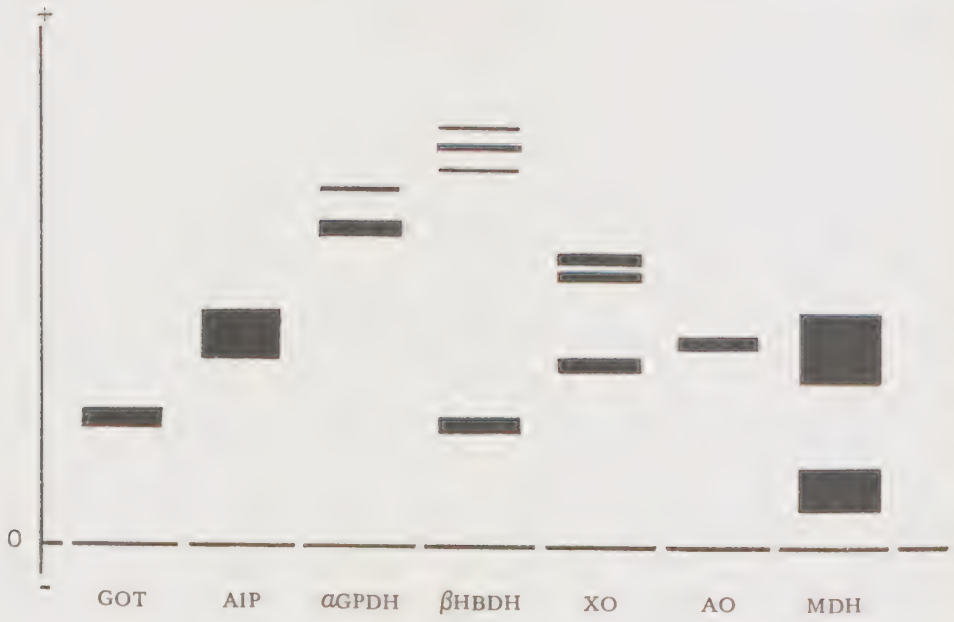

FIG. 1. Schematic diagram of various enzyme patterns in *Bulinus truncatus*. Patterns shown are glutamate oxaloacetate transaminase-1 (GOT), alkaline phosphatase (AlP), α-glycerophosphate dehydrogenase-1 and -2 (αGPDH), β-hydroxybutyrate dehydrogenase-1 and -2 (βHBDH), xanthine oxidase-1 and -2 (XO), aldehyde oxidase (AO) and malate dehydrogenase-1 and -2 (MDH).

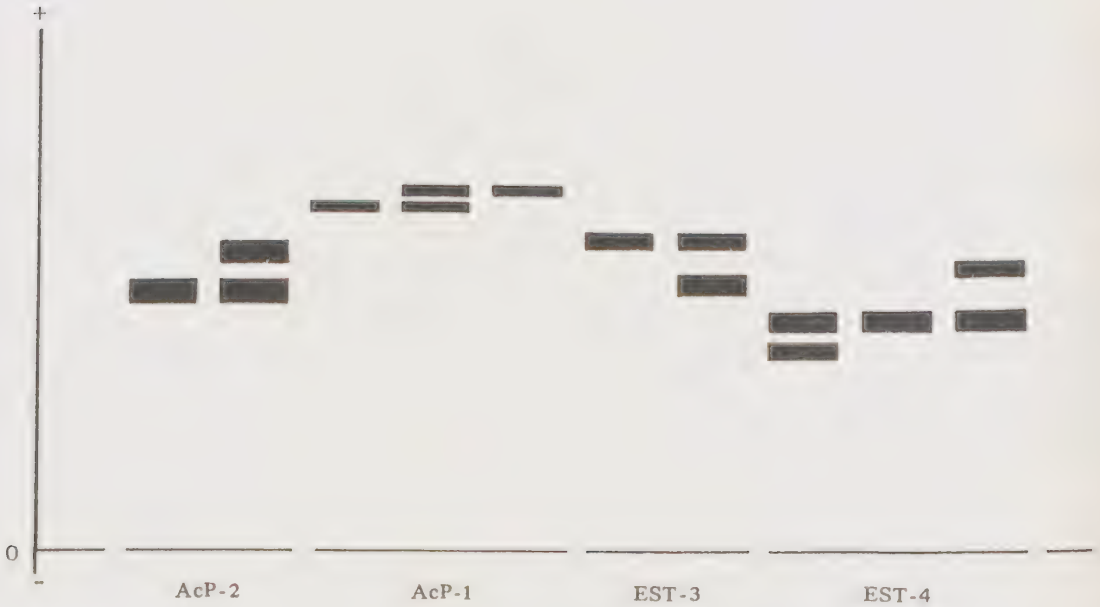

FIG. 2. Schematic diagram of various enzyme patterns in *Bulinus truncatus*. Patterns shown are acid phosphatase-2 (AcP-2) ($2^{1.00}/2^{1.00}$, $2^{1.00}/2^{1.13}$); AcP-1 ($1^{1.00}/1^{1.00}$, $1^{1.00}/1^{1.09}$, $1^{1.09}/1^{1.09}$); esterase-3 (EST-3) ($3^{1.00}/3^{1.00}$, $3^{0.84}/3^{1.00}$) and EST-4 ($4^{1.00}/4^{1.13}$, $4^{1.13}/4^{1.13}$, $4^{1.13}/4^{1.40}$).

FIG. 3. Non-specific esterases of *Bulinus truncatus* from Egypt (1-4), Jordan (5-8), Syria (9-12) and Ethiopia (13-16) detected with α-naphthyl acetate as substrate. The various zones recognized are numbered to the right. EST-5 is not detected with this substrate.

substrates. EST-7 developed as a single, sharp band of activity in all four populations. There may be a quantitative difference in this enzyme because the staining intensity of this band in the Jordanian population was less than in the other three populations. The remaining three zones of non-specific esterase activity showed some interpopulation variation. However, intrapopulation variation in these enzymes was not detected. EST-1 contained two alleles. The Ethiopian, Egyptian and Jordanian populations all possessed the slow 1.00 allele, whereas the Syrian population possessed the slightly faster 1.04 allele. EST-3 was another diallelic system. It is the major activity detectable with αNB and is not detected with βNA. The Egyptian and Ethiopian populations were monomorphic for the fast 1.00 allele, while the Jordanian and Syrian populations also contained the slower 0.85 allele in addition to the 1.00 allele. EST-4 is a multi-allelic system. It is the major activity detected with αNA and βNA. It is not detected with αNB. Three different phenotypes were observed. The Ethiopian population possessed alleles 1.00 and 1.13. The Jordanian and the Syrian populations both possessed the 1.13 allele, and the Egyptian population possessed alleles 1.13 and 1.40.

Acid phosphatase (AcP) (buffer systems I, III). Two regions of acid phosphatase activity were detected. AcP-1 is a variable enzymatic activity containing two alleles. The Ethiopian, Egyptian and Jordanian populations were monomorphic for the slow 1.00 allele. No inter- or intrapopulation variation of this enzymatic activity was detected among these three populations. The Syrian population contained an additional, faster (1.09) allele. For the Syrian population, this enzymatic activity may be interpreted as a codominant diallelic system with two-banded heterozygotes and gene frequencies of 0.70 and 0.30 for the 1.00 and the 1.09 alleles. The observed phenotypic ratio of one fast homozygote : four two-banded heterozygotes : five slow homozygotes agrees closely with Hardy-Weinberg expectations for large outbreeding populations.

AcP-2 is another variable enzymatic activity containing two alleles. The Egyptian and the Ethiopian populations were monomorphic for the slow 1.00 allele, whereas the Jordanian and the Syrian populations contained an additional faster allele. All individuals of the latter

two populations contained both the 1.00 and the 1.15 alleles. No intrapopulation variation of this enzymatic activity was detected.

Alkaline phosphatase (AlP) (buffer systems I, III). A single broad band of activity referable to this enzyme was detected in all individuals examined. No variation within or between populations was found.

Glutamate-oxaloacetate transaminase (GOT) (buffer systems I, II, III). Two monomorphic regions of GOT activity were detected in all individuals examined. GOT-1 migrates anodally in all three buffer systems. GOT-2 was only adequately resolved in buffer system III, in which it migrates cathodally.

α-glycerophosphate dehydrogenase (αGPDH) (buffer systems I, II, III). Two weak zones of activity referable to this enzyme were detected in all the individuals examined. They were designated tentatively as monomorphic αGPDH-1 for the fast band and monomorphic αGPDH-2 for the slower band.

β-hydroxybutyrate dehydrogenase (βHBDH) (buffer system I). Two regions of βHBDH activity were detected in all individuals examined. No variation within or between populations was observed. βHBDH-1 consisted of a three-banded region which is interpretable as a diallelic system with heterodimer formation in heterozygotes. All the individuals examined appear to be fixed heterozygotes. βHBDH-2 contained a single band of activity in all individuals examined. It was monomorphic in these populations.

Malate dehydrogenase (MDH) (buffer systems I, II, III). This enzymatic activity was poorly resolved by all systems examined. Addition of NAD to the electrode and gel buffers improved resolution somewhat. Two broad regions of NAD-dependent MDH activity were detected in all individuals examined. These are designated tentatively as MDH-1 and MDH-2. MDH-2, the slow region, migrated cathodally in buffer system III. It had some activity with NADP as cofactor and thus may be the malic enzyme. Only one variant was detected. This individual, which was the Syrian snail infected with the unidentified eye-spotted cercariae, had one additional band of MDH-1 activity. This band had a mobility of 0.6 relative to the 1.00 MDH-1 band.

Xanthine oxidase (XO) (buffer system II or III). Two regions of XO activity were detected with hypoxanthine as substrate. No intra- or interpopulation variation was detected. XO-1, the fast region, contained two closely spaced bands of activity, and XO-2, the slow region, consisted of a single band of activity.

Aldehyde oxidase (AO) (buffer system II or III). Two bands of activity were detected with benzaldehyde as substrate. The slow band occupied the same position as XO-2 and thus may be that enzyme. The fast band of activity was designated as AO. No intra- or interpopulation differences were detected.

Hemoglobin (Hb) (buffer systems I, II, III). A single, invariant, monomorphic band referable to this protein was detected in all individuals examined. No variation within or between populations was detected.

DISCUSSION

Our results indicate that, of the 22 presumptive genetic loci belonging to 10 different enzymatic activities or proteins, only two esterases and perhaps acid phosphatase are of potential use in determining the origin of the Jordanian *Bulinus*. The snails found in Jordan were typical *B. truncatus*, in that they were tetraploid, i.e., they had 36 pairs (2n=72) of chromosomes, and they were all aphallic, a condition which is very common in *B. truncatus*. No differences among the four populations examined were detected in 17 or the 22 presumptive genetic loci analyzed. Only acid phosphatase (two loci) and esterases (three loci) showed some interpopulation variation, and only acid phosphatase-1 of the Syrian population showed some intrapopulation variation.

The Jordanian and the Syrian snails differed from the African snails in esterase-3 and esterase-4, as well as acid phosphatase-2. Although acid phosphatase-1 is a variable enzyme in the Syrian population, about half of the snails used do have the same enzyme band as the Jordanian and the African populations. The Jordanian *Bulinus* do differ from the Syrian snails in esterase-1 and possibly esterase-7. Malate dehydrogenase is potentially an interesting enzyme because of the variant found in the infected Syrian snail. It needs to be determined if this additional band is a normal variant of the Syrian *Bulinus* or if it is due to infection by the parasite.

At this time we are unable to specify the origin of the Jordanian *Bulinus*. Egypt may be ruled out due to the difference in the euphallic/aphallic condition and due to the differences in the esterase and acid phosphatase isozymes. Although the Jordanian *Bulinus* are closer genetically to the Syrian snails than to the African ones, their allozyme patterns are not identical and thus the snails found in Jordan probably were not introduced from Syria. Further work using populations from various countries in that geographic region is needed and is now being planned.

ACKNOWLEDGEMENTS

We would like to thank the Director and staff of the Syrian Schistosomiasis Control Center for collecting and making available to us the Syrian *Bulinus*, and Dr. J.B. Burch for support and for verifying the chromosome numbers of the snails used in this investigation.

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K.-H. WURZINGER
Museum of Zoology and Division of Biological Sciences
The University of Michigan
Ann Arbor, Michigan 48109, U.S.A.

E.K. SALIBA
Department of Biological Sciences
University of Jordan
Amman, Jordan

Malacological Review, 1979, 12: 67-78

CALCIUM CELLS AND GROOVE CELLS IN CALCIUM METABOLISM IN THE FRESHWATER LIMPET *FERRISSIA WAUTIERI* (BASOMMATOPHORA: ANCYLIDAE)

Monique Richardot

ABSTRACT

The connective tissue becomes heavily loaded with calcium cells just before estivation or hibernation in *Ferrissia wautieri*. When external mineralization is rapid (septum or shell formation), soluble calcium salts are present in the extracellular spaces of the connective tissue, in intercellular spaces of the dorsal epithelium of the mantle and in ovocytes. Moreover, the groove cells of the connective tissue take up extracellular calcium by means of the groove system and contain calcium salts in various concentrations.

INTRODUCTION

The presence of calcium deposits occurring as intracellular granules have been found in a large number of molluscan tissues. However, the mechanisms involved in intracellular calcification, the functions of these granules in the organism and the different routes of calcium salt movement are not really understood (see Simkiss, 1976).

The freshwater limpet *Ferrissia wautieri*, which has a particular biological cycle, represents very suitable material for the study of calcium metabolism in molluscs.

It has been established that, in a population of this freshwater limpet, certain individuals are able to develop a drought resistant form (Richardot, 1974, 1976). In this species, all hatching juveniles are typical ancylids, but, in summer, after hatching, the development may proceed in two different ways according to ecological conditions. Either the conditions are favourable, in which case the individual grows and reproduces without changing the shape of the shell, or the conditions are unfavourable (i.e., drought), in which case the animal develops a septum before it starts to breed. This septum is a thin calcareous layer, partially closing the shell aperture[1]. When conditions again become favourable, the animal starts to form a new shell, growth taking place from the edge of the constricted aperture, thus giving the shell a distinctly different shape throughout life. A limpet which follows the second course passes through three successive stages: "ancyloid", "septifer" and "postseptifer".

In the cold season, reproduction stops and shell secretion is considerably reduced. All the individuals of the population hibernate under such conditions.

In a previous paper (Richardot & Wautier, 1972), it has been stated that, in *Ferrissia wautieri*, calcium is stored in the intracellular spherule of calcium cells. These calcium cells are particularly numerous in the mantle and between the central nervous system and the upper part of the foot. The spherules consist of calcium carbonate deposited on an organic matrix. The calcium carbonate is either amorphous or crystallized in the form of vaterite or aragonite, but may crystallize as calcite during hibernation or estivation. The calcospherites have a spherolithic structure (both concentric and radial crystalline structure). They are generally complex, with several nuclei.

It has been stated that the aspect, the number, the volume, and the rate of crystallization of the calcospherites are different according to the season. It may therefore be assumed that the characteristics of the spherules are connected with metabolic variations in this animal.

[1] It has been shown that there is a complete similarity in crystalline structure between shell and septum in *Ferrissia* (Richardot et al., 1972).

It has been pointed out that the connective tissue becomes heavily loaded with calcospherites, just before estivation or hibernation. The whole reserve will disappear with the resumption of growth and reproduction when the external circumstances are favourable again (Richardot & Wautier, 1972; Richardot, 1976). But, at the same time, some new spherules are formed to constitute a "normal" new storage.

We are now able to initiate and to remove estivation in *Ferrissia* at will under laboratory conditions (Richardot, 1977b, c, 1978). Thus it is possible to obtain (1) a conspicuous increase in number of intracellular spherules in immatures reared in unfavourable conditions, and (2) a rapid external mineralization, either during septum formation or during growth of the new shell after cessation of estivation.

In the present paper, some results are presented with respect to calcium deposits in the mantle of *Ferrissia*, and hypotheses are forwarded as to the function of these deposits in calcium metabolism.

METHODS

For fixation, the shell was removed and appropriate segments of the body (posterior part of the mantle) were dissected out in the fixing fluid. The pieces excised were fixed either in 2% osmium tetroxide or in 3% glutaraldehyde and postfixed in 2% osmium tetroxide. The fixing fluids were buffered with cacodylate-HCl, pH 7.4. The final osmolarity of the medium was 250 mOsm. Pieces were embedded in Epon. Ultrathin sections were stained with a saturated solution of uranyl acetate in methanol, followed by lead citrate. They were examined in a Philips E.M. 300 electron microscope.

The electron microscope histochemistry of calcium was performed with lead acetate according to the method of Carasso & Favard (1966). The pieces were fixed in 3% glutaraldehyde in phosphate buffer (pH 7.8) for one hour at 4°C. The fixed material was rinsed in distilled water in which the pH was adjusted to 8.0 with NaOH just before use. Then pieces were incubated in 0.5% lead acetate for 15 minutes at 37°C. After being briefly rinsed in distilled water, they were postfixed in 2% osmium tetroxide in cacodylate-HCl buffer for one hour. Ultrathin sections were stained with uranyl acetate only.

Controls were performed by decalcification of prefixed pieces in glutaraldehyde, either with an EDTA disodium salt solution buffered according to Kashiwa (1966) or with 0.4 M sodium citrate buffer, pH 4.8, according to Carasso & Favard (1966).

The light microscope histochemistry of soluble calcium salts were performed with Glyoxal-bis (2 hydroxyanil) (GBHA) according to the method of Kashiwa (1966). The animals were immersed in liquid nitrogen. The cryostat sections (10-15 μ) were stained for two minutes, the reagent being prepared just prior to use by adding 0.1 g of GBHA in 2 cc of a standard solution (3.4% NaOH in 75% ethanol). The slides were rinsed in 75% ethanol. The best results were obtained by *in toto* staining. The animals were immersed directly in the reagent, then dissected in 75% ethanol and observed.

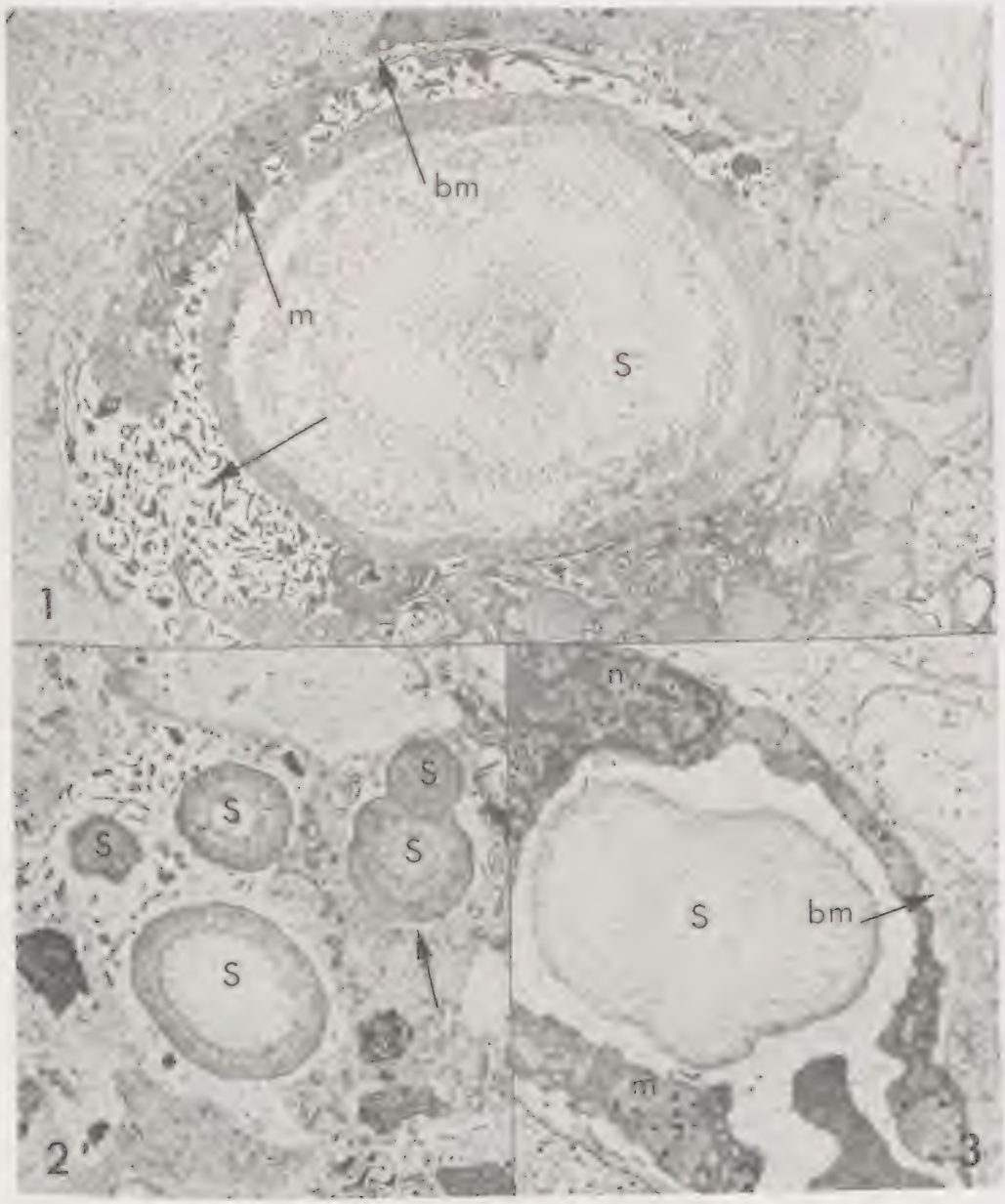
RESULTS

Calcium cells

After normal fixation and uranyl acetate staining, the calcium cell spherules indicated concentric ring arrangement of fibrous material. It is likely that the calcium salts were removed during specimen preparation and that the fibrous material represents the organic matrix.

The calcium cell spherule is surrounded by a thin layer of cytoplasm which is disrupted in places. This layer of cytoplasm is thicker in the nuclear region, where degenerating mitochondria with numerous electron dense granules can be observed (Fig. 1), associated with triglycerides, glycogen and ribosomes. The cytoplasm at this cell pole is generally disorganized. Vestiges of membrane, smooth endoplasmic reticulum and cytoplasm are scattered in disorder. These features are particularly striking in young calcium cells, in which the spherule is not so large in regard to the cell volume (Fig. 1). In all calcium cells, the surrounding layer of cytoplasm and the cell membrane are disrupted and the spherule is separated from the extracellular spaces only by the basal membrane which is always present (Fig. 1).

In a previous paper (Richardot & Wautier, 1972), the calcospherites have been described. In the present study, we shall only provide some new observations about the young spherules.



FIGS. 1-3. Young calcium cells, fixed in osmium tetroxide. FIG. 1. Arrow, disorganized cytoplasm. x8,100. FIG. 2. Arrow, membrane of a spherulite vacuole. x10,500. FIG. 3. x9,000.
bm, basal membrane; m, mitochondria; n, nucleus; s, spherulites; S, spherule.

Young calcospherites indicate different structures according to their stage of development. The most developed ones have a spherolithic structure. Radially disposed fibrils are first noticed in the periphery (Figs. 2, 6). Before this stage, the concrement center is fibrous or finely reticular with a more dense external layer (Fig. 3). The smallest calcospherites are situated in a vacuole (Fig. 2), but this is not clear for the larger ones.

In tissues stained for calcium with lead acetate, electron dense deposits are observed in calcium cells. The deposits appear in three concentric layers in the calcospherites: an outer

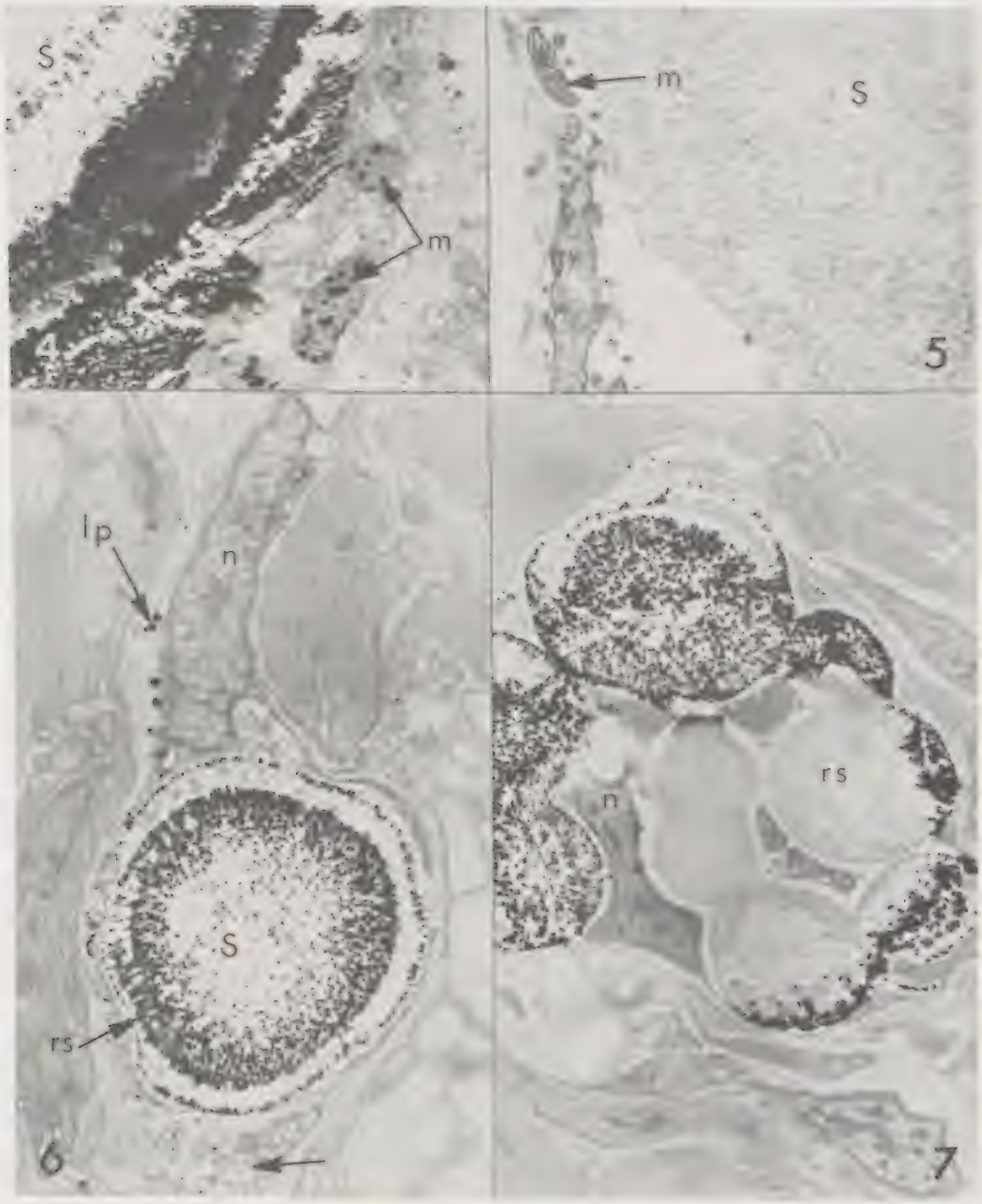


FIG. 4. Three different external layers of a spherule in a calcium cell. Carasso & Favard technique. x14,000. FIG. 5. External layers of a spherule in a calcium cell. Lead acetate incubation after decalcification (control). x30,000. FIG. 6. Young calcium cell with one spherule. Arrows, disorganized cytoplasm. Carraso & Favard technique. x10,800. FIG. 7. Young calcium cell with several spherules. Carasso & Favard technique. x6,000.

lp, lead precipitates in the extracellular space; m, mitochondria; n, nucleus; rs, beginning of the radial organization; S, spherule.

layer, which consists of bundles of crystalline needles, a middle layer of closely packed crystals, and an inner, fibrous layer (Fig. 4). One or two of these three layers may be lacking (Fig. 16). In the spherule center, bundles of very fine needles can be seen (Figs. 6, 7).

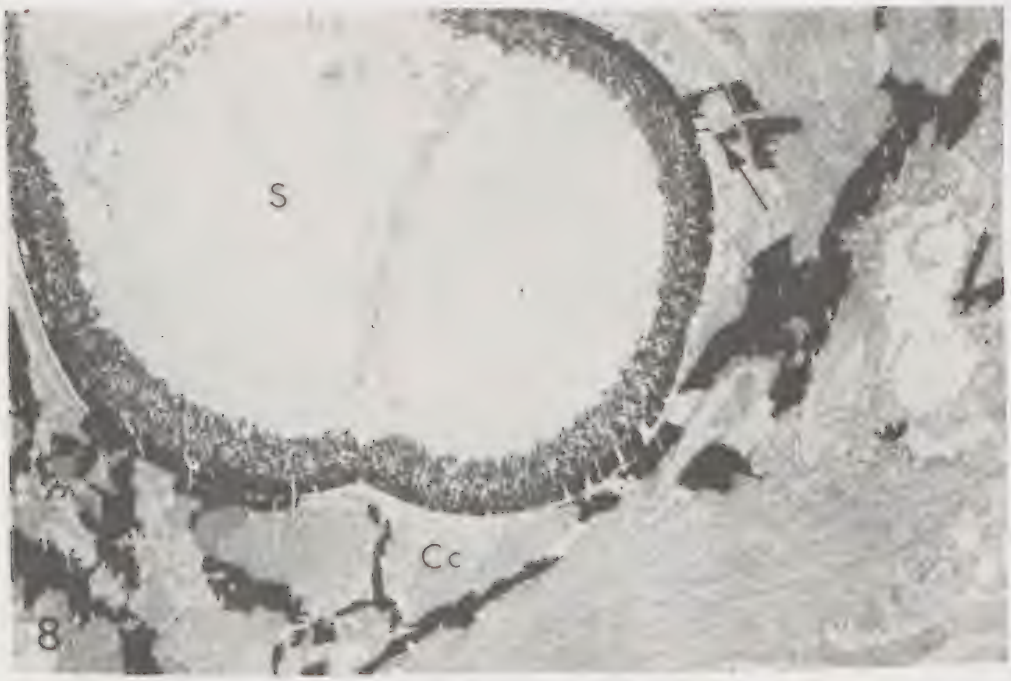


FIG. 8. Dense lead deposits in extracellular spaces around a calcium cell, in the calcium cell (arrow) and on the surface of the calcospherite. S, complex calcospherite; Cc, cytoplasm of the calcium cell. Carasso & Favard technique. x6,400.

Dense deposits are observed in the extracellular spaces, in and around the calcium cells (Fig. 8). As distance from the calcium cells increases, the reaction is weaker and the extracellular spaces contain a variable number of electron dense granules or needles.

In tissues stained after decalcification (control), deposits are completely absent from the calcospherites and the extracellular spaces. On the other hand, a fine electron dense deposit

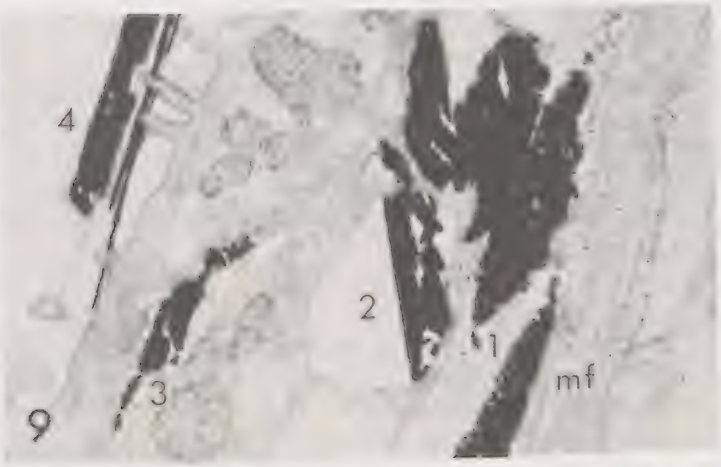


FIG. 9. Dorsal epithelium of the mantle. Animal with a septum in the course of construction (septum length = 0.08 mm). Dense lead deposits in extracellular spaces lining the epithelium (1), in the large vesicles at the bottom of the epithelium cells (2), in the intercellular spaces (3), on the epithelium surface (4). mf, longitudinal muscular fibres. Carasso & Favard technique. x20,700.

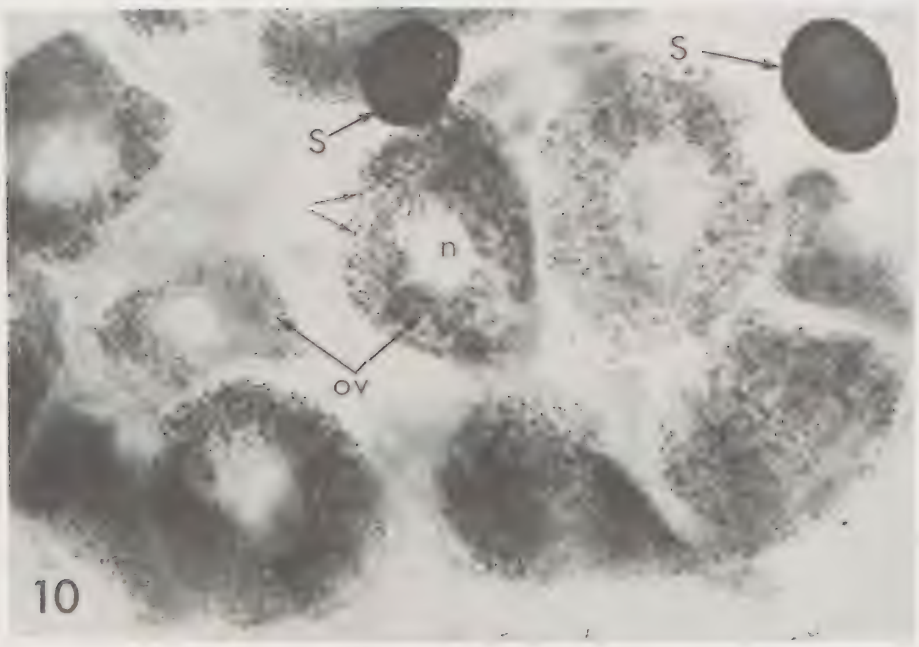


FIG. 10. Staining of the soluble calcium salts in the gonad. Animal killed after the removal of estivation, just before first egg laying. n, nucleus; ov, ovocytes; S, spherule of the connective tissue around the gonad. Positive reaction on the spherule's surface, and in the ovocytes (arrows). Kashiwa technique, animal directly immersed in the reagent. x1,555.

can be found on the cell and endoplasmic reticulum membranes and on the mitochondria cristae (Fig. 5).

The dorsal epithelium of the mantle

In *Ferrissia*, the outer side of the mantle is lined with a low columnar epithelium. These cells are linked by septate desmosomes. The intercellular spaces often are winding and locally enlarged. When growth is rapid, the inner cell membrane is folded up and it forms large vesicles lining the epithelium basal membrane (Richardot, 1976).

After incubating tissue in lead acetate, dense precipitates can be observed in the dorsal epithelium of the mantle both in animals killed before estivation (septum formation) and after the removal of estivation (new shell growth). The precipitates line the dorsal epithelium; moreover, the large vesicles at the bottom of the epithelial cells and the intercellular spaces are labelled (Fig. 9). In some cases a dense layer can be seen on the epithelium surface (Fig. 9).

Ovocytes

In animals killed after the removal of estivation, just before the deposition of the first batch of eggs, the Kashiwa (1966) technique of staining soluble calcium salts always provides positive results in the gonad. The larger ovocytes are labelled with a characteristic red staining (Fig. 10).

Groove cells

"The groove-cells are characterized by a differentiation of the plasma membrane whose surface seems ploughed by long, narrow (220 Å) winding grooves. These grooves correspond in reality to clefts which let large peripheric cytoplasmic vacuoles communicate with the exterior of the cell" (Pavans de Ceccatty & Nicolas, 1975).

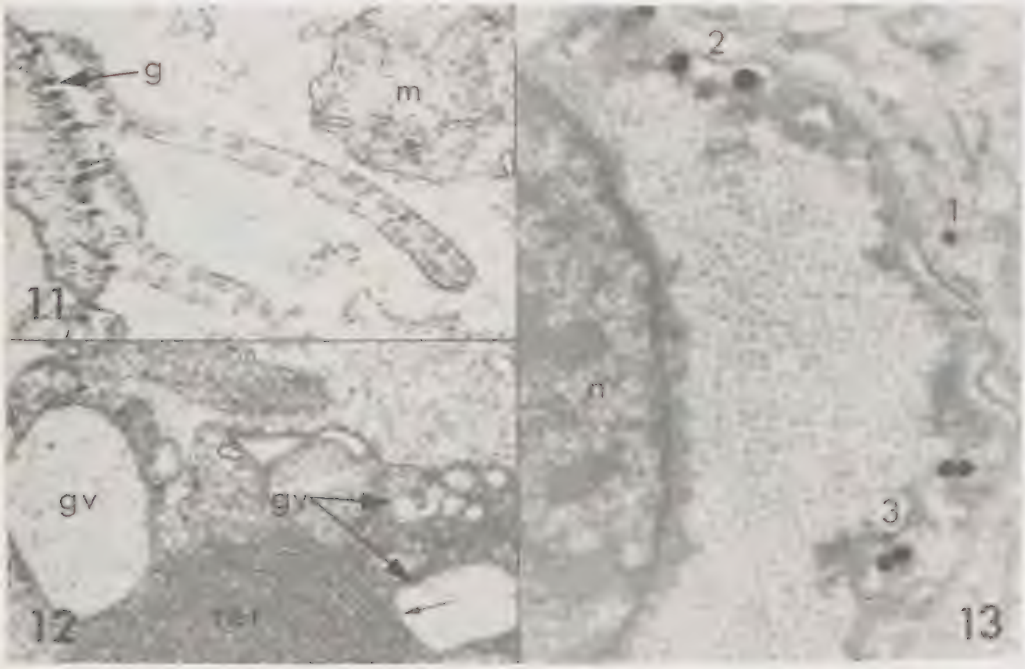


FIG. 11. Tubules of the smooth endoplasmic reticulum in communication with the groove system. Fixation, osmium tetroxide. x43,000. FIG. 12. Groove cell. Arrows, fine material lining the groove system membranes. Fixation, glutaraldehyde and osmium tetroxide. x13,000. FIG. 13. Small spheres of lead precipitate in the extracellular space (1), in a groove (2), in the groove cell cytoplasm (3). Carasso & Favard technique. x17,000.

g, groove; gv, groove system underlying vacuoles; m, mitochondria; n, nucleus; rer, rough endoplasmic reticulum.

This cell type has been described in molluscs by several authors who used different terms for it: globular cells or vesicular cells (Rogers, 1969; Schmekel, 1972; Wolburg-Buchholz, 1972a,b; Dyer & Cowden, 1973), pore-cells (Plummer, 1966; Sminia, 1972; Sminia & Boer, 1973), brown cells (Ruddell & Wellings, 1971) or fibroblast (Nicaise et al., 1966).

In *Ferrissia*, groove cells are present in the connective tissue, especially between the central nervous system and the upper part of the foot, and in the posterior mantle. These cells are always surrounded by a basal membrane (Fig. 16). They contain various amounts of polysaccharide deposits. In young cells the glycogen is only sparsely distributed in the cytoplasm which is rich in rough endoplasmic reticulum. In larger cells the groove system is poor. The polysaccharide deposits are spread in larger patches. The smooth endoplasmic reticulum tubules are widely distributed and some of them communicate with the groove system (Fig. 11). There is a thin layer of fine material all around the inner surface of the tubule membrane. This same fine material also lines the membrane of the grooves and of the vacuoles underlying the groove system. Irregularly shaped vesicles of various dimensions can be observed in the cytoplasm. The analysis of various micrographs led us to consider those vesicles as groove system elements. The smallest vesicles appear empty, but their membrane is lined with the same fine material as in the groove (Fig. 12). The larger ones appear to be filled with a lightly staining, amorphous substance (Fig. 13). In the most inflated vesicles the content is finely fibrous and an electron dense area can be observed centrally. Mitochondria have distorted cristae and the matrix contains numerous osmiophic granules (Richardot, 1977a).

After incubating the tissue in lead acetate, lead deposit granules can be observed in the extracellular spaces. These granules may be found in contact with the outer surface of the cell membrane of the groove cells, in the grooves and in the cytoplasm underlying the cell membrane (Fig. 13).

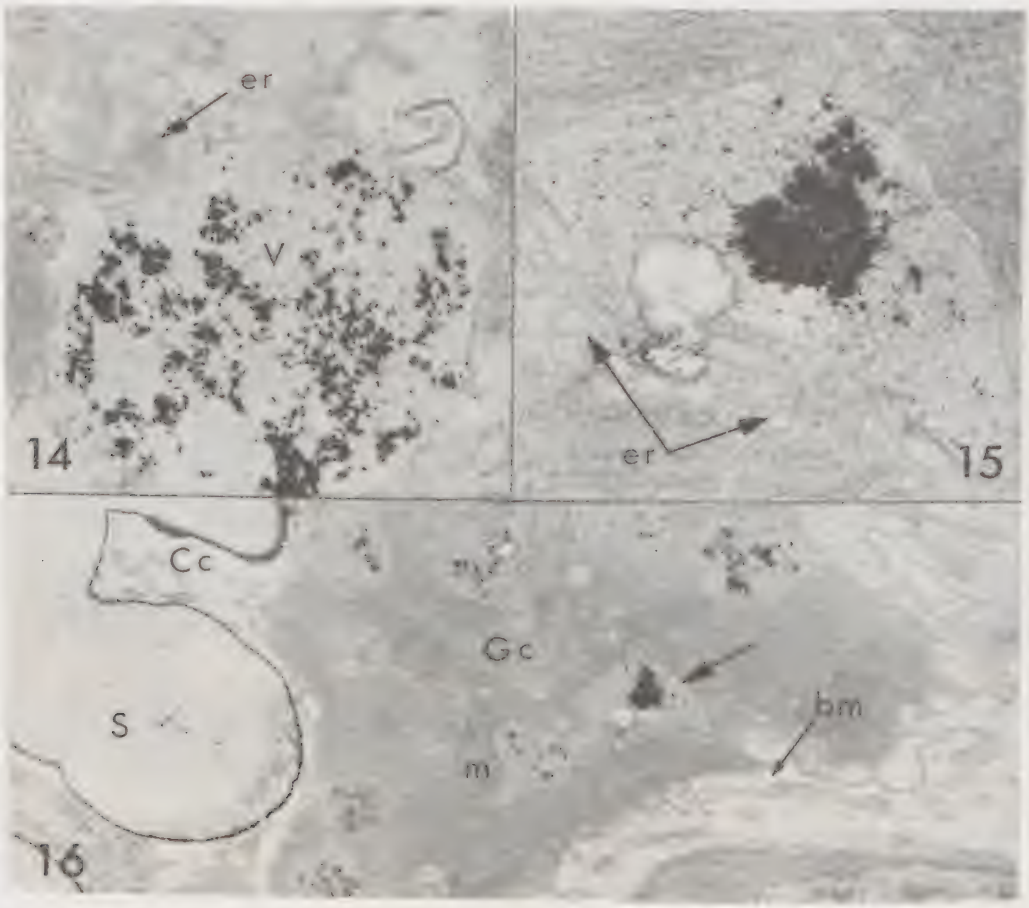


FIG. 14. Vacuole of a groove cell. Note the close contact of a smooth endoplasmic reticulum element and the vacuole membrane. Carasso & Favard technique. x40,000. FIG. 15. High magnification picture of the vesicle shown in Fig. 16. x50,000. FIG. 16. Vacuole content of a groove cell stained by lead precipitates. Arrow, vesicle shown in Fig. 15. Carasso & Favard technique. x11,200.
bm, basal membrane; Cc, calcium cell; er, smooth endoplasmic reticulum; Gc, groove cell; m, mitochondria; S, spherule; V, vacuole.

The content of the large vesicles in the groove system gives a positive reaction with lead acetate. The content of the smaller vesicles is also stained. The limiting membrane of these vesicles is extremely irregular and communicates with the smooth endoplasmic reticulum (Figs. 14, 15, 16).

After decalcification (control), these precipitates are lacking and only a faint staining of the membranes of the different cells and organelles can be observed.

DISCUSSION

Several hypotheses have been forwarded as to the function of calcium cells in molluscs. Firstly, it has been suggested that calcium of the granule may provide a store for external mineralization (shell, operculum or epiphragm) (Prenant, 1924; Wagge & Mittler, 1953; Kapur & Gibson, 1968; Saleuddin, 1970; Haley & Gibson, 1971; Abolins-Krogis, 1968, 1972). Unfortunately, the evidence on this is relatively sparse. In *Lymnaea stagnalis*, the calcium granules seem not to be implicated in shell mineralization even though growth is rapid (Timmermans, 1969). Secondly, as has been stated by Nieland & Brand (1969) and Chowdhury & de Rycke (1974) for cestodes, a role of these granules in the pH homeostasis

of the organism has been proposed (Burton, 1970; Istin & Girard, 1970; Greenaway, 1971b; Van der Borght & Puymbroeck, 1971; Istin & Masoni, 1973; Sminia et al., 1977). A third physiological function has been proposed by Kniprath (1975): the calcium granules might play a role in protein catabolism.

With respect to the calcium movements, in some cases, it has been stated that calcium-rich granules are transported around the body and to the mantle in amoebocytes (Wagge, 1951; Wagge & Mittler, 1953; Abolins-Krogis, 1968, 1972; Saleuddin, 1970; Neff, 1972). In other cases, it has been shown that the extracellular fluids may be supersaturated with calcium ions (Burton, 1970; Greenaway, 1971a,b). Such an interpretation raises the question of the inhibition of crystallization in the body fluids (Bachra & Fischer, 1969; Simkiss, 1976).

It is generally accepted that the epithelium of the mantle is implicated in calcium transfer in molluscs, but the routes of movement of calcium salts are mostly unknown. Neff (1972) and Vovelle (1973) have provided strong arguments in favour of the presence of calcium in intercellular spaces of the mantle epithelium in *Mercenaria mercenaria* and *Astrea rugosa*, whereas Kniprath (1971) and Istin & Masoni (1973) show presence of calcium only in the cytoplasm of the epithelium cells in *Lymnaea stagnalis* and in bivalves.

The description of calcium cells in *Ferrissia wautieri* (Richardot & Wautier, 1972) is, in general terms, similar to that of other calcium cells in molluscs described more recently (Tompa & Watabe, 1976; Sminia et al., 1977).

In the present paper, the observation of young calcium cells with several small spherulites shows that the initial concretions form in membrane-bound vesicles as it is generally observed (Fauré-Frémiet, 1957; Bouillon, 1960; Abolins-Krogis, 1965, 1968; Gouranton, 1968; Nieland & Brand, 1969; Pautard, 1970; Walker, 1970; Sminia et al., 1977). Then the large spherules with several nuclei observed in the connective tissue are likely the result of accretion of several initial spherulites.

According to Carasso & Favard (1966), the lead acetate method reveals soluble or easily ionisable calcium carbonate or phosphate.

After incubating tissues in lead acetate, several large calcospherites are only stained on the outer surface. The various aspects of the staining of the spherules might represent different stages in the crystallization of the calcium carbonate, as it has been previously observed with other methods (Richardot & Wautier, 1972). This might account for the presence of staining in the center of young calcospherites.

As it has been observed by Carasso & Favard (1966), tissues showed a faint staining on membranes, after decalcification. As discussed by the authors, this might indicate a reaction of the lead salt with organic phosphates. However, the striking difference observed between the slight staining of the control and the large deposits widely distributed in non-decalcified tissues is thought to be significant enough to assume the presence of calcium salts.

After incubating tissues in lead acetate, the localization of conspicuous extracellular precipitates around calcium cells confirms the idea of soluble calcium salt movement in the extracellular spaces of the connective tissue[2]. The intracellular granules never extrude from the cell.

The dense deposits observed in the extracellular spaces, as in the cytoplasm of the calcium cell and on the spherule surface, led us to consider that there is a relationship between the extracellular calcium and the calcium of the spherule.

These results and the conspicuous decrease in the number of spherules in the connective tissue after the removal of estivation (Richardot, 1976) suggest that intracellular calcium deposits might be released into extracellular spaces as soluble calcium salts. Thus, such a releasing is connected with the resumption of growth and reproduction. We have also provided some data to show presence of soluble calcium salts in two other sites: the mantle epithelium involved in the shell or septum formation, and the ovocytes, when reproduction occurs. These observations, then, suggest that the calcium released might be used for external mineralization and for the calcium loading of ovocytes, but conclusive evidence is still lacking

[2]With a light microscope, similar results have been obtained with Kashiwa staining (Richardot, 1976).

to support this view.

If our presumptions are correct and confirmed by further investigations, the calcium cells might play a role of calcium storage in *Ferrissia*. As has been stated by Sminia et al. (1977), calcium cells have a function in pH homeostasis in another freshwater pulmonate, *Lymnaea stagnalis*. Is it not conceivable that a cell type may have several functions?

It is now generally accepted that several functions can be attributed to groove cells in molluscs (Pavans de Ceccatty & Nicolas, 1975): (1) fibroblastic activities (Nicaise et al., 1966; Plummer, 1966); (2) osmotic regulation (Ruddell & Wellings, 1971; Wolburg-Buchholz, 1972a,b; Boer et al., 1973); (3) synthesis of blood pigment (Sminia, 1972; Sminia et al., 1972; Jong-Brink, 1973; Skelding & Newell, 1975); (4) polysaccharide storage (Rogers, 1969; Sanchis & Zambrano, 1969; Dyer & Cowden, 1973; Jong-Brink, 1973); (5) pigment cell activities (Sullivan et al., 1974).

Moreover, it seems likely that, in *Ferrissia*, these cells are capable of taking up extracellular calcium salts. After incubating tissues in lead acetate, small spheres of lead precipitate can be seen in contact with the groove cell membrane and in the groove system. This may account for the presence of these small spheres in the peripheral cytoplasm. These results are in agreement with those of Wolburg-Buchholz (1972a,b), Pavans de Ceccatty & Nicolas (1975) and Skelding & Newell (1975), who reported that molecules such as ferritin can be captured by the grooves.

The content of some vesicles of groove cells has been stained by lead acetate. These vesicles are either vacuoles underlying the groove system or vesicles in communication with the smooth endoplasmic reticulum. It can be inferred from the structural relationships observed that the groove system is in communication with the smooth endoplasmic reticulum. Lead precipitates can also be observed in the cytoplasm. The accumulation of calcium salts in mitochondria of these cells may be connected with an increase in the intracellular calcium concentration (Sampson et al., 1970; Brinley, 1973; Richardot, 1977a).

Thus, without further available information, we can only suppose that groove cells take up extracellular calcium by means of the groove system, and contain calcium salts in various concentrations. Then the groove cells might have a role in calcium metabolism in *Ferrissia wautieri*.

It can be inferred from previous observations (Richardot, 1976) and the present results that, in *Ferrissia*, the calcium economy consists of a complex regulatory system which maintains an equilibrium between the different calcium compartments in the organism: external and internal milieux, intracellular spherules, external calcareous sheaths (shell and septum), kidney and ovocytes (Richardot, 1976, 1979).

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MONIQUE RICHARDOT

Laboratoire de Biologie animale et Zoologie and
Centre de Microscopie Appliquée à la Biologie et à la Gèologie
Université Claude Bernard - Lyon I
43, Bd du 11 Novembre 1918
69621 Villeurbanne, France

Malacological Review, 1979, 12: 79-84

EXTRUSIVE GENITAL ANATOMIES AND THEIR INTERNAL POSTURES IN *PARTULA AFFINIS* OF TAHITI

Yoshio Kondo and J.B. Burch

ABSTRACT

From observations on the anatomy of the extruded phallus, spermatheca and vagina of *Partula affinis*, the following assumptions are made regarding the role of these structures during copulation. The everted penis contacts and adheres to the everted spermatheca of the mating partner, filling the spermatheca and depositing the spermatophore when the spermatheca invaginates by penial stimulation. The everted spermatheca embraces the protruding phallus, enfolds it, then invaginates fully to receive the spermatophore internally. The vagina everts in concert with the spermatheca and acts as a guide tube for the phallus in reaching the spermatheca. Sperm migrate from the spermatophore via the inverted vagina following copulation.

INTRODUCTION

This paper describes the anatomy of the extruded genital organs (phallus, spermatheca and vagina) of *Partula affinis* Pease of Tahiti, French Polynesia. These observations lead to a clearer picture of the functional relationships of the copulatory organs during mating.

MATERIALS

Source material for the dissections described in this study were nine specimens from station 1970-195, collected by J. B. Burch and company (James N. Cather, John B. Burch, Jr. and Evin Oshima) in Faaripoo Valley, Tahiti, 23 July 1970. Collection 195 consists of *Partula* collected while walking home at the end of the day and covers a 2 kilometer stretch of territory collected earlier in the day as stations 191 to 194.

In collection 195 were the following: (a) 77 adult *Partula affinis* and four juveniles, among which were 41 adults with genital extrusions having one, two or three orifices, and 36 normal non-extrusives; (b) 23 unextruded *P. otaheitana rubescens* Reeve; and (c) two unextruded *P. hyalina* Broderip. Other instances of *P. affinis* having extruded genitalia were noted from other stations. In other species, extrusions have been rare.

The *Partula affinis* of Tahiti described here are a small part of an extensive collection of Partulidae made during 1966-70 in Melanesia and Polynesia with National Science Foundation Grants GB-3974 and GB-6450, 1965-71. These materials have been incorporated into the collections of the Bernice P. Bishop Museum, Honolulu. (The anatomical monograph of family Partulidae is scheduled for completion by December 1980.)

OBSERVATIONS

In genital extrusions of *Partula affinis* Pease, the phallus, spermatheca and vagina are protruded completely out of the body cavity to their fullest extent.

The phallus everts completely to form an elongate proboscis-like narrow cone or a bulb. Internally, eversion occurs right up to the orifice of the vas deferens, at which place the penial retractor meets the epiphallus (Fig. 4 P). The internal surface of the epiphallus and phallus turn inside-out to become the outer skin or sheath of this cone. In copulation, this pointed penial cone is presumed to contact and to adhere to the everted spermatheca, and it becomes the spermatheca's internal occupant when the spermatheca invaginates by penial stimulation. In this fully invaginated posture, the penis deposits its load of spermatophore; the penis then withdraws unilaterally without the assistance of the spermatheca.

The spermatheca everts completely, becoming a proboscis-like protrusion also, but having a truncate apex (Fig. 4 O). The oval pouch of a normal spermatheca turns inside-out when everted and becomes the skin or sheath of the spermatheca. The truncate apex

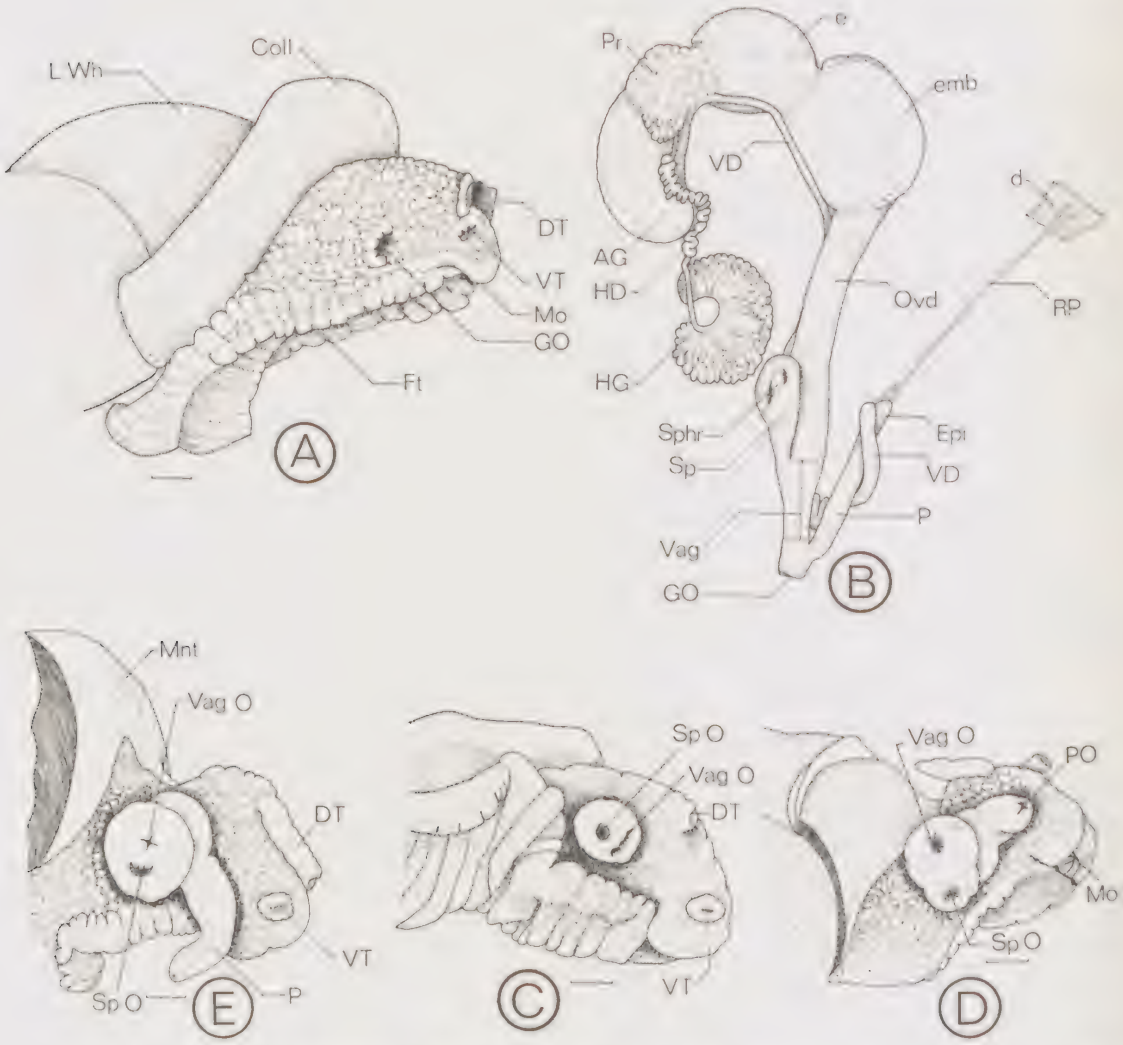

FIG. 1. A, Anterior 3/4 view of *Partula affinis* illustrating a simple normal genital orifice (GO) for comparison with Figs. 1 (C, D, E) and Fig. 2 (F, G), which have extrusions at the genital orifice.

B, Normal dextral genitalia of *Partula affinis* to compare with Fig. 2 (H) and Fig. 3 (M). The spermatheca is a short internal bulb standing upright against the oviduct; the rip in the spermatheca shows a cylindrical spermatophore. The extent of the vagina is shown in dashed lines from the root of the spermatheca to the atrium. The phallus is short, tubular and narrow; the vas deferens enters the epiphallus subapically; the penial retractor connects at the tip of the epiphallus.

C, Extruded genitalia with two orifices: the spermathecal and vaginal orifices on a single bulbous body which represents the everted internal wall of the genital orifice and atrium (compare with Fig. 1 (D, E) and Fig. 2 (F, G)).

D, Specimen with three genital orifices: the vaginal and spermathecal orifices on two closely connected bulbs; the penial orifice on a third distantly connected bulb.

E, Specimen with three genital orifices: the vaginal and spermathecal orifices on a single spherical bulb; the penial orifice on the apex of a prolonged proboscis-like conical tube through which the phallus is dimly visible.

Abbreviations: AG, albumen gland; Coll, collar; d, diaphragm; DT, dorsal tentacle; e, egg; emb, embryo; Epi, epiphallus; Ft, foot; GO, genital orifice; HG, hermaphrodite gland or ovotestis; HD, hermaphrodite duct; L Wh, last whorl; Mnt, mantle; Mo, mouth; Ovd, Oviduct; P, phallus or penis; Pr, prostate gland; P Sh, penial sheath or skin; RP, penial retractor; R Sp, spermathecal retractor; Sp, spermatheca; Sphr, spermatophore; Sp O, spermathecal orifice; Ut, uterus; Vag, vagina; Vag O, vaginal orifice; VD, vas deferens; VDO, orifice of vas deferens into epiphallus; VT, ventral tentacle.

Measurement lines = 1 mm.

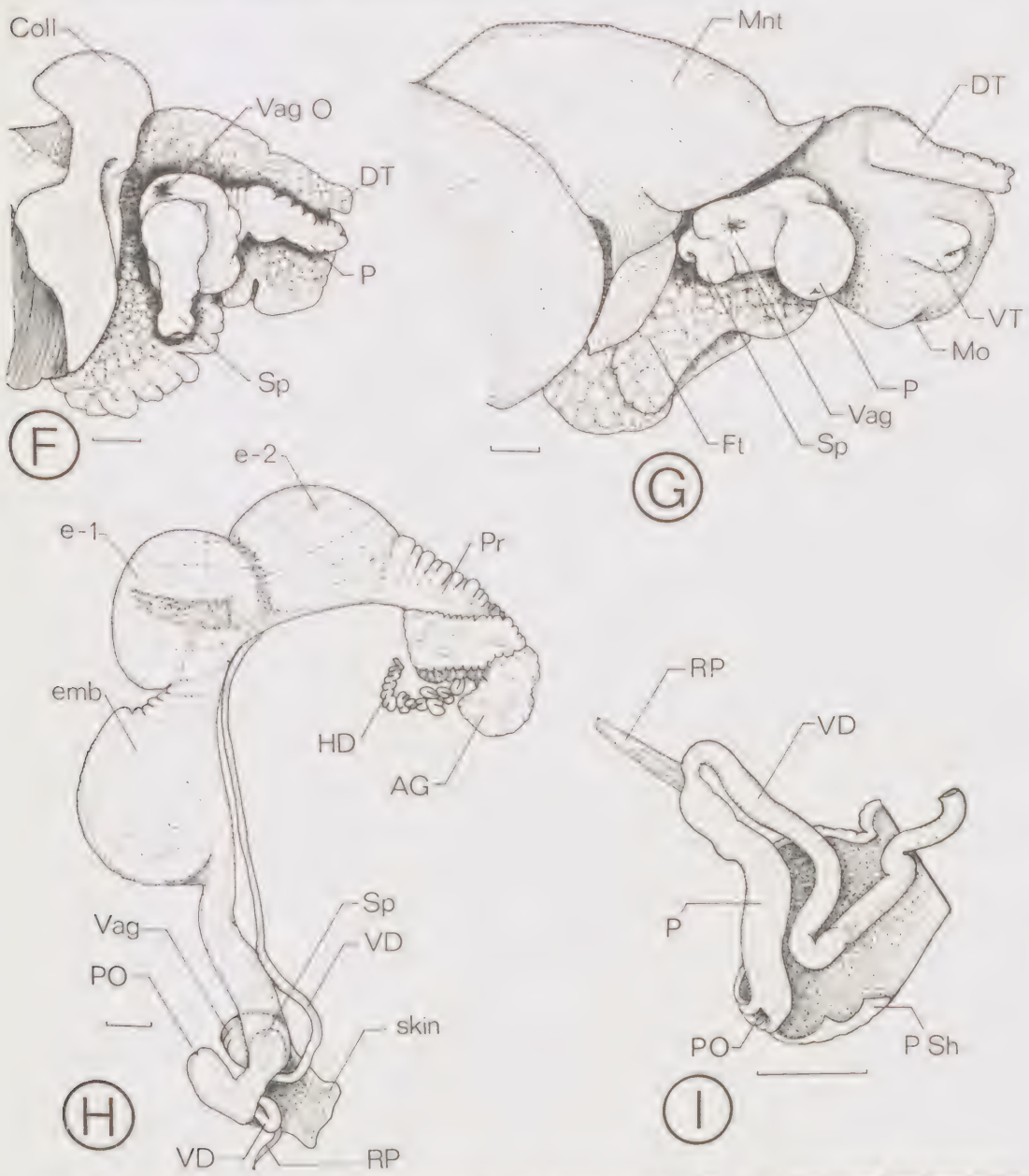

FIG. 2. **F**, Specimen with three genital orifices: the spermathecal orifice on a prolonged proboscis-like conical protuberance, truncated at the apex; the vaginal orifice on a bulb; the penial orifice on a prolonged conical wrinkled extrusion. Internal anatomy in Fig. 3 (M, N) and Fig. 4 (O, P, Q) in fullest protrusion.

G, Anterior 3/4 view of fourth *Partula affinis* specimens with all three genital orifices extruded: penial bulb with the phallic tube visible from the outside (cf. Fig. 2 (I)); vaginal and spermathecal orifices on adjacent closely associated bulbs facing posteriad. Internal anatomy in Fig. 2 (H, I) and Fig. 3 (J, K, L) in partial extrusion.

H, Genitalia of Fig. 2 (G), reverse view, which reveals (in Fig. 2 (I) and Fig. 3 (J, K, L)) the posture of the phallus, spermatheca and vagina in a half-extruded genitalia. The spermatheca and 2/3 of the vagina are hidden behind the free oviduct. The skin is opened to reveal the vas deferens curving to enter the penial sheath. First egg, e-1; second egg, e-2.

I, The protruding phallic bulge is opened to reveal the posture of the phallus, penial retractor, and vas deferens internally. The phallus is not everted fully; it is capable of everting further as in Fig. 4 (P).

See legend to Fig. 1 for key to abbreviations. Measurement lines = 1 mm.

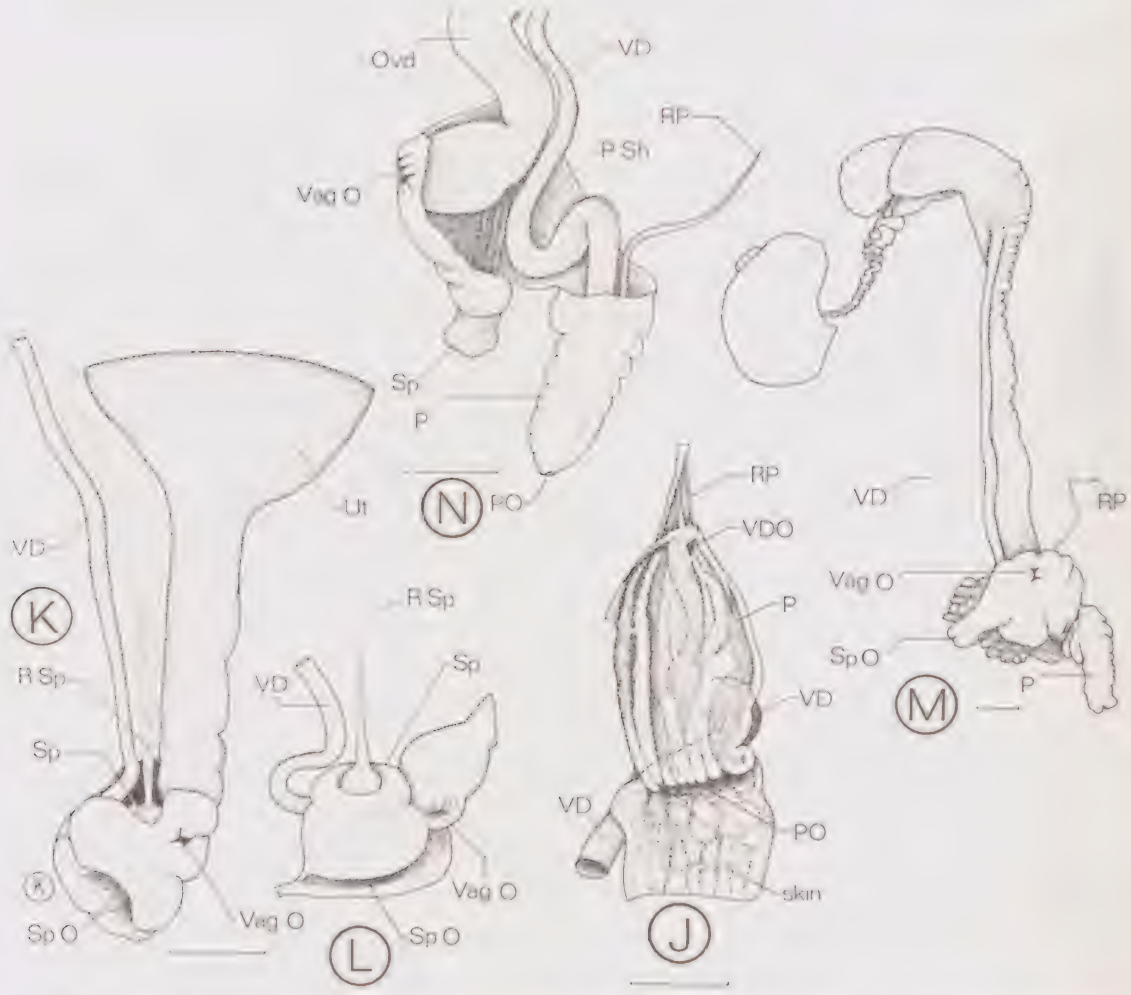

FIG. 3. **J**, Phallus cut open vertically to reveal one well-defined vertical ridge (second from left) and three parallel weak ridges. These ridges disappear when complete eversion takes place and the inner wall becomes the outer skin or sheath. The epiphallus is usually minutely and sparsely tuberculate in *Partula affinis*, but in this specimen pustules are either obscured or absent. The vas deferens located behind the phallus is outlined in dashed lines.

K, Closeup of the lower portion of Fig. 1 (H); the spermatheca and vagina are exposed to view, in part. The spermatheca is extruded from its normal posture (cf. Fig. 1 (B)), but not all the way. The retractor of the spermatheca is a conspicuous but delicate series of fibrillar threads which anchor on the oviduct and vas deferens and converge at the head of the spermatheca to form a fairly solid retractor there. The semi-extruded spermatheca is an inconspicuous bulb hidden between the oviduct and the vas deferens and requires search. The spermathecal and vaginal orifices are close together. The spermathecal orifice is surrounded by skin inflated into a circumferential lip.

L, Spermatheca cleanly denuded of obstacles to reveal its contracted semi-extruded shape. The tit sits inside a shallow dimple atop a bulbous contracted spermatheca; from this tit arises a delicate pointed retractor which becomes delicate flimsy fibrilles distally. In full extrusion, the spermatheca should look like Fig. 4 (O).

M, Internal genital anatomy of Fig. 2 (F) from which the phallus, spermatheca, and vagina are shown fully extruded and a section of the interior of the vas deferens exposed (in Fig. 3 (N) and Fig. 4 (O, P, Q)). The tip of the animal housing the ovotestis is attached to the hermaphrodite duct.

N, Internal organs and their posture in partial revelation prior to full exposure (in Fig. 4 (O, P)). The wide separation between the vagina and spermatheca indicates that the vagina can extrude just as much as the phallus and spermatheca (cf. Vag in Fig. 1 (B)). Much of the vaginal wall becomes the external skin. Fibrillar tissues forming the spermathecal retractor are just visible. The wrinkled proboscis-like phallus is semi-transparent and the vas deferens can be seen through the skin.

See legend to Fig. 1 for key to abbreviations. Measurement lines = 1 mm.

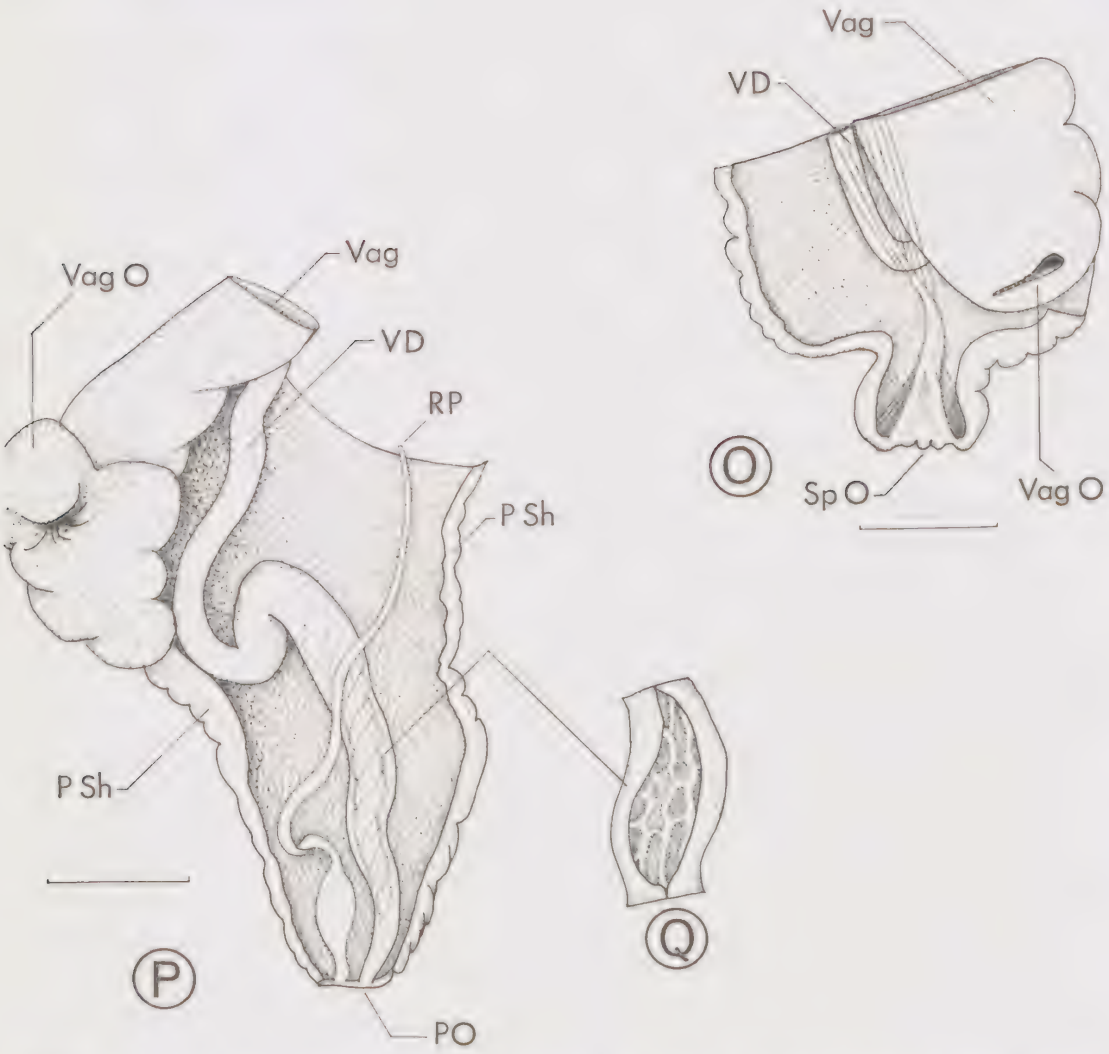

FIG. 4. O, The spermatheca is completely everted, its orifice a triangular dead-end cavity (shown shaded), recessed into a tiny triangular internal tit which forms the apex of the normal spermatheca and the base of its retractor. The retractor becomes flimsy and fibrillar above to anchor on the vas deferens and vagina. The inner cavity of the normal oval spermatheca (cf. Fig. 1 (B)) is now the skin of the inside-out truncated protrusion (cf. Fig. 2 (F)).

P, Interior topography of the penial extrusion in *Partula affinis* (cf. Fig. 3 (N)) opened up completely to reveal the vas deferens terminating at the tip of the inverted protrusive penial cone. The outer surface of the penial cone is actually the extruded penial interior (cf. Fig. 3 (J)), now serving as the penial sheath. The end of the vas deferens is joined side by side at the apex of the cone by the terminus of the penial retractor. The normal posture of this assembly may be visualized by examining the phallic assemblage in Fig. 1 (B) and Fig. 2 (I).

Q, Interior of the vas deferens. When seen through its thin integument (Fig. 4 (P)), the interior of the vas deferens appears like a rope where the strands are twisted evenly into each other, but, when a longitudinal incision is made into the tube and the cut end spread wide and pinned down (Fig. 4 (Q), freehand sketch), the interior surface appears differently: the surface consists of a series of vertically oriented low fleshy ridges which anastomose with each other via short fleshy spurs to form a delicate network.

To picture Fig. 4 (P) as being returned to its normal retracted posture (cf. Fig. 2 (I)), the penial sheath must be visualized as invaginating from the very tip of the inverted cone. Both the retractor and the tip of the vas deferens then pull inward and upward in concert while simultaneously the skin oozes inward and upward to become the interior of the penis (cf. Fig. 3 (J)).

See legend to Fig. 1 for key to abbreviations. Measurement lines = 1 mm.

has a tiny triangular cavity in its center that internally forms the tip of the spermathecal retractor muscle. It is presumed that the everted spermatheca embraces the protruding phallus of its partner in copulation, enfolds it, then invaginates fully to receive the spermatophore internally. The spermatheca is a storehouse for the spermatophore, from which sperm migrate via the vagina to fertilize the eggs within the oviduct.

The vagina extrudes fully in concert with the spermatheca, but no special structure distinguishes it internally or externally except a shortened duct internally and a spherical bulb externally having an orifice in it. In mutual copulation, it is presumed that the vagina functions naturally as a guide tube by way of which the copulating partner's phallus enters the spermatheca for the purpose of depositing the spermatophore there.

All the above presumptions remain as such until proven by first hand observations.

Partial and maximal phallic-spermathecal extrusions are illustrated in Figs. 1-4. The full story is given in chronological sequence in the figure legends, so discussion in the text below is minimal.

For comparison with extrusives (Figs. 1 C-E, 2 F,G), external and internal aspects of a normal *Partula affinis* are given (Fig. 1 A,B).

In partial extrusion (Figs. 2 G-I, 3 J-L), the phallus protrudes with the penial bulge, but remains unevaginated (Figs. 2 H,I, 3 J). Simultaneously, the spermatheca shortens internally, its normal ovate pouch now shrunken into a tiny tit submerging into a bulbous base (Fig. 3L); and where formerly no positive retractor was visible, now there is a definite slender tapering retractor which ends distally as fine delicate fibrilles. Externally, the base of the spermatheca becomes a great fat lip (Fig. 3 K) surrounding a dead-end cavity (Sp O). The vaginal tube shrinks to nothing, its external manifestation is a swollen bulge with an orifice in it. The three organs are now ready for full extrusion.

In full extrusion (Figs. 3 M,N, 4 O,P), the phallus becomes a proboscis-like conical tube externally and the spermatheca a truncate tube. Internally, the phallus everts to the limit (Figs. 3 N, 4 P); its internal wall now becomes its external skin or sheath (Fig. 4 P) with no resemblance at all to its internal topography (cf. Fig. 3 J). Simultaneously, the fully extruded spermatheca (Fig. 4 O) becomes a truncated cone, the internal wall of its pouch turning inside-out to become its skin or sheath. Its tip and retractor assembly form a produced pyramid, the external base of which in-pockets into a short triangular cavity (Fig. 4 O, Sp O, shaded triangle) which properly is not an orifice at all but a dead-end invagination.

The cause of these interesting extrusions is not known positively, but may be ascribed to (a) artificial stimulation by unnatural conditions of confinement in a crowded 500 cc plastic bottle, limited air, jouncing along the trail, a rise in temperature and atmospheric pressure at sea level from the cool forested heights inland; or (b) a natural response to sexual stimulation caused by overcrowding and an inability to retract to normal posture during the killing (by drowning) period.

ACKNOWLEDGEMENTS

We are indebted to the Government of French Polynesia, in particular to the Director of ORSTOM, Office de la Recherche Scientifique et Technique Outre Mer, Dr. Henri Lavondes, who had tenure in 1970.

YOSHIO KONDO
J.B. BURCH

Bernice P. Bishop Museum
Honolulu, Hawaii 96818, U.S.A.

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CAMPELOMA PARTHENUM (GASTROPODA: VIVIPARIDAE), A NEW SPECIES FROM NORTH FLORIDA. – Comprehension of the North American viviparid genus *Campeloma* Rafinesque is still quite superficial. The most recent revision of species is that by Call (1886), although several nominal species and subspecies have since been described. With the exception of Anderson's (1966) brief historical summary of the generic taxonomy of *Campeloma*, recent studies on the genus have been faunal surveys (Clench & Turner, 1956), anatomical studies (Vail, 1977) and life history observations (Vail, 1978). Species identification, based on shell characteristics as interpreted from usually brief and vague original descriptions, is made more difficult by a poor understanding of both the environmental effects on shell morphology and the animals' habits.

Although Wurtz & Roback (1955) reported *Campeloma lewisii* from the Escambia River, according to Clench & Turner (1956), only *C. geniculum* Conrad is found in northwestern Florida. *C. floridense* Call is unique to the St. Mary's and St. John's river systems in northeastern Florida. However, another *Campeloma*, which by virtue of its appearance, reproductive habits and geographical distribution is distinct from other north Florida *Campeloma*, has been recognized. This entity is herein named *Campeloma parthenum* in recognition of its reproductive habits.

Campeloma parthenum sp. nov. (Fig. 1). Shell medium to large sized, maximum shell diameter up to 25 mm (Little River specimens), but usually about 19 mm (Lake Talquin and Ochlockonee River specimens); color light green, luster dull; apical erosion common, precluding use of shell length measurements as an index of size. Spire elongate; whorls sharply set off from one another; shoulders flattened. Shell adjacent to sutures smooth when viewed from the apex. Sides of whorls only slightly convex, giving shell a slender appearance. Elliptical aperture not laterally flared, giving aperture a narrow appearance, but the anterior ("ventral") margin is slightly flared to the left of the columellar axis. Center half of outer lip of aperture straight and parallel to columellar axis. Aperture rounded at base but not broadly. Shell color inside aperture uniformly white. Reproduction parthenogenetic. Shell color of newborn uniformly white.

FIGS. 1-4. Shells of *Campeloma*; all scales are 5 mm. FIG. 1. Holotype of *C. parthenum* from Coe's Landing on Lake Talquin, Leon County, Florida. FIG. 2. *C. geniculum* from the Chipola River at Florida Highway-167, Jackson County, Florida. FIG. 3. *C. limum* (UMMZ 230519) from Dickinsons Creek, Ben Hill County, Georgia. FIG. 4. *C. floridense* from Orange Creek, Putnam/Marion County line, Florida.

Type locality: Lake Talquin (impoundment of Ochlockonee River) at Coe's Landing, about 21 km west of Tallahassee (off Florida Highway-20), Leon County, Florida. Known distribution: This species is currently known only from the Ochlockonee River drainage: Lake Talquin, upstream in the Little River to Florida Highway-268 and upstream in the Ochlockonee River to Federal Highway-90. Holotype (Fig. 1): UMMZ 250053. Shell length, 30.2 mm; shell diameter, 17.5 mm; aperture length, 16.2 mm; aperture diameter, 10.8 mm; apex eroded but five whorls present. Paratypes have been deposited in the University of Michigan, Museum of Zoology (UMMZ), the Academy of Natural Sciences, Philadelphia, and the Florida State Museum, Gainesville.

Habitat: In contrast to the predominantly sandy or clay substrates from which I have collected *Campeloma geniculum, C. floridense* and *C. limum, C. parthenum* seems to prefer a mucky substrate common to Lake Talquin, the Little River and back water coves of the Ochlockonee River. Occasionally *C. geniculum* is found with *C. parthenum* in coves in the Ochlockonee River, but does not occur in Lake Talquin or the Little River. *C. geniculum*, common to sandy portions of the main river channel, is not abundant in these coves, and *C. parthenum* has been found in the main river channel only near the Lake Talquin impoundment.

Campeloma parthenum can be readily distinguished from *C. geniculum* (Fig. 2) by the presence in the former of the straight outer margin of the aperture paralleling the columellar axis, the overall slender appearance (i.e., sides of whorls only slightly convex and aperture not laterally flared), the leftward flare of the anterior (ventral) aperture margin and the dull luster. The length of the aperture in relation to body whorl length is less in *C. parthenum* than in *C. geniculum* of equivalent diameters. Also, reproduction in *C. parthenum* is presumably parthenogenetic as no males have been found among the more than 3000 specimens observed in the last eight years. This reproductive method is in contrast to *C. geniculum* in which males are common.

Campeloma parthenum can be distinguished from *C. limum* (Fig. 3), another parthenogenetic species in drainages of the southern Atlantic Slope, by the presence in the former of the straight outer margin of the aperture paralleling the columellar axis, the overall slender appearance of the shell, the leftward flare of the ventral margin and the smooth shell in the region of the sutures. In *C. limum*, a small portion of the laterally flared outer aperture margin can be straight but it is at an angle to the columellar axis and there are faint traces of sutural angulations when the shell is viewed from the apex.

Campeloma parthenum can be distinguished from *C. floridense* (Fig. 4) by the presence in the former of the straight outer aperture margin, an overall slender appearance, more flattened shoulders, the leftward flare of the ventral (anterior) aperture margin, elongate spire and the white shell of newborn young. In *C. floridense* the sides of the whorls and outer aperture margin are convex, the shoulders are more rounded, the spire is short and the entire shell of newborn young (but only the interior of the aperture of adults) is brown.

Preliminary observations on the nervous system organization, male and female reproductive anatomy and brood production lend at least provisional support for recognizing the taxa employed here. A comparative study of the anatomical systems of *Campeloma*, in progress, and electrophoretic investigations, soon to be initiated, will aid in further interpretation of the relationships within this genus.

Acknowledgements. I wish to acknowledge W.H. Heard, Florida State University, for his assistance in collecting some of the specimens examined and for his comments on the manuscript, and Phil Ashler, Jr. and G.W. Hanning for their help with the photography.

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VIRGINIA A. VAIL, *Tall Timbers Research Station, Rt. 1, Box 160, Tallahassee, Florida 32312, U.S.A.*

A PRELIMINARY REVISION OF FLORIDA *LIOPLAX* (GASTROPODA: VIVIPARIDAE), WITH A DESCRIPTION OF *LIOPLAX TALQUINENSIS* SP. NOV. – Four geographically isolated species have previously been recognized in the North American viviparid genus *Lioplax*: *L. sulculosa* Menke from eastern Minnesota south to northeastern Arkansas and east to southern Ohio-northern Kentucky; *L. subcarinata* Say from central New York south to South Carolina; *L. cyclostomaformis* Lea in the Alabama River drainage in Alabama and northwestern Georgia and in the Tensas River in Louisiana; and *L. pilsbryi* Walker from the Choctawhatchee River to the Suwannee River in northern Florida and north into central Georgia in the Appalachicola drainage system, viz., in the Flint and Chattahoochee tributaries (based on Clench & Turner, 1955; Clench, 1962; and personal collections). *L. pilsbryi choctawhatchensis* Vanetta 1935, described from a seasonally isolated lentic tributary (Horseshoe Lake) of the lower Choctawhatchee River, was considered by Clench & Turner (1955) to be synonymous with *L. pilsbryi* s.s.

According to Vanetta's (1935) description, the only character distinguishing *Lioplax pilsbryi choctawhatchensis* (Fig. 1) from *L. pilsbryi* s.s. (Fig. 2) is the considerably smaller size of the former. Spiral shell sculpture is similar between the two forms, although in *L. pilsbryi* s.s. the dorsally located angulation on each whorl is most prominent in younger specimens; in older specimens that angulation tends to be more smooth and convexly rounded. In addition, preliminary anatomical observations show ctenidial structure and certain aspects of brood production to be similar. In both taxa the filaments are long and narrow (lanceolate) and the females incubate comparatively small broods in the pallial oviduct (generally less than 20 young). The differences in brood production appear to be a reflection of the distinct size difference between the two entities. Female *L. p. choctawhatchensis* are mature (as indicated by the presence of incubating young in the pallial oviduct) at a shell diameter of less than 10 mm; maximum diameter of the adult rarely exceeds 13 mm. In contrast, female *L. p. pilsbryi* are rarely mature at a shell diameter of less than 15 mm (Vail, 1978), and the reproductive system in females less than 13 mm in diameter is not completely developed; maximum shell diameter can reach 18 mm. The shell diameter of newborn *L. p. choctawhatchensis* is approximately 3.0 mm; young of *L. p. pilsbryi* are approximately 4.5 mm in diameter at birth (Vail, 1978). Also, the large *L. p. pilsbryi*, found only in the Chipola River tributary of the Apalachicola River drainage, are geographically exclusive from the smaller (dwarfed?) *L. p. choctawhatchensis* of the Flint and Chattahoochee river tributaries of the same drainage system as well as from the Escambia, Choctawhatchee and Suwannee river drainages. I consider these distinctions sufficient to warrant recognition of these two entities as subspecies, and I herein elevate *L. p. choctawhatchensis* from prior synonymy under *L. pilsbryi* Walker. Ongoing anatomical and impending electrophoretic investigations will hopefully further clarify the status of these taxa.

Further examination of the northern Florida *Lioplax* fauna shows that one common shell form is distinctly different from that of the large *L. pilsbryi* s.s. and the smaller *L. p. choctawhatchensis*. This form is herein named *Lioplax talquinensis* after the locality at which it was first recognized as unique.

FIGS. 1-4. Shells of Florida *Lioplax*; all scales are 5 mm. FIG. 1. Ventral view of *L. pilsbryi choctawhatchensis* from Horseshoe Lake, Washington County, Florida, topotypes. FIG. 2. Ventral view of *L. p. pilsbryi* from the Chipola River at Florida Highway-167, Jackson County, Florida (for reproductive anatomy and patterns see Vail, 1977, 1978). FIG. 3. Ventral view of holotype of *L. talquinensis* from Coe's Landing on Lake Talquin, Leon County, Florida. FIG. 4. Dorsal view of same specimen as Fig. 3.

Lioplax talquinensis sp. nov. (Figs. 3, 4). Shell medium-sized, with maximum diameter usually about 11 mm and only rarely greater; color light green, but occasionally obscured by mineral deposition (Yellow River); apical erosion variable, precluding use of length measurements as an index of size. Whorls sharply set off from one another; shoulders of whorls flattened to slightly rounded; sides of whorls only slightly convex, giving shell a slender appearance. Elevated subsutural spiral sulcus present on body whorl, prominent in Ochlockonee drainage populations but less distinct elsewhere; lacking spiral angulations; shape of aperture subovate, distinctly narrower dorsally. Type locality: Lake Talquin (impoundment of Ochlockonee River) at Coe's Landing, about 21 km west of Tallahassee, Leon County, Florida. Known distribution: Ochlockonee River (Lake Talquin and upstream to Federal Highway-27, about 18 km north of Tallahassee) and

Yellow River (northwestern Florida and southern Alabama) drainages. Holotype: UMMZ 250056. Shell length, 14.7 mm; diameter, 9.1 mm; aperture length, 7.6 mm; aperture diameter, 5.2 mm; 5 whorls. Paratypes from Lake Talquin and the Yellow River at Federal Highway-90 in Okaloosa County, Florida, have been deposited at the Museum of Zoology, University of Michigan (UMMZ), Academy of Natural Sciences, Philadelphia, and the Florida State Museum, Gainesville.

Lioplax talquinensis is immediately differentiated from *L. pilsbryi* s.l. by the presence in the former of a shallow to prominent elevated subsutural spiral sulcus on the body whorl and by the dorsally narrowed, elliptical aperture. Also, the outer lip of the aperture in *L. pilsbryi* s.l. is seen to be conspicuously sinuous when the shell is positioned apex up and with the aperture facing to the left, whereas the outer aperture lip in *L. talquinensis* is only slightly sinuous.

Although observations on anatomical characters are as yet incomplete, it appears that the short, broad, relatively thick ctenidial filaments in *Lioplax talquinensis* are distinct from the long, narrow, thin ctenidia in *L. pilsbryi* s.l. In addition, female *L. talquinensis* carry a much larger brood of young in the pallial oviduct. For example, 100 young were removed from a female *L. talquinensis* that was 9.0 mm in diameter; shell diameter of the young at birth is approximately 1.5 mm. Female *L. pilsbryi* s.s., which can be up to twice as large in diameter, incubate less than 20 young that are born with a shell diameter of approximately 4.5 mm (Vail, 1978); as already noted above, brood sizes in *L. p. choctawhatchensis* are similar and the shell diameter of newborn is about 3.0 mm.

Shells of *Lioplax pilsbryi choctawhatchensis* from the Suwanee River initially resemble those of *L. talquinensis* because of the presence on them of a subsutural spiral sulcus, but they have spiral angulations as in *L. pilsbryi* s.l. (none in *L. talquinensis*). Moreover, ctenidial filaments of these Suwannee River specimens resemble those of *L. pilsbryi* s.l. and not those of *L. talquinensis*.

Two other medium-sized species of *Lioplax* are found in the southern United States: *L. subcarinata* and *L. cyclostomaformis*. *L. subcarinata* is distinguished from *L. talquinensis* by the presence in the former of two peripheral angulations located on the body whorl, shoulders sloping upwards to the suture, a more convex body whorl, and the aperture which is more rounded than elliptical in shape and dorsally rounded. *L. cyclostomaformis* has an overall slender appearance and a shell diameter within the range described for *L. talquinensis*. It can be distinguished from *L. talquinensis* by a greater length of the body whorl, more convex sides, rounded shoulders and shallow sutures, whorls only gradually decreasing in diameter toward the apex, and a subelliptical aperture that is broadly rounded at both ends and that is dorsally set sharply off from the body whorl. In some specimens of *L. cyclostomaformis* the aperture appears to be more ventrally located in relation to the body whorl in contrast to the more lateral location seen in *L. talquinensis*. The anatomy of *L. cyclostomaformis* is unknown.

Preliminary studies of ctenidia, nervous system organization, male and female reproductive anatomy and brood production lend at least provisional support for recognizing the taxa employed here. A comparative study of the anatomical systems of *Lioplax*, in progress, and electrophoretic investigations, soon to be initiated, will aid in further interpretation of the relationships of these viviparids.

Acknowledgements. I wish to acknowledge W.H. Heard, Florida State University, for his assistance in collecting some of the specimens examined and for his comments on the manuscript, and Phil Ashler, Jr. and G.W. Hanning for their help with the photography.

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VIRGINIA A. VAIL, *Tall Timbers Research Station, Rt. 1, Box 160, Tallahassee, Florida 32312, U.S.A.*

THE NATURE OF AGGREGATIONS OF *NASSARIUS OBSOLETUS* IN THE INTERTIDAL ZONE BEFORE THE FALL OFFSHORE MIGRATION. – Migrations of *Nassarius obsoletus* into deeper waters at the onset of colder weather in temperate climates seem to be a regular feature of their life histories (Batcheldor, 1915; Jenner, 1956, 1957, 1958, 1959; Sinderman, 1960, 1961; Scheltema, 1964). I observed migrations from the intertidal zone at Jamaica Bay in November of 1974, 1975, 1976 and 1977. Crisp (1969) and Jenner (1956, 1957, 1958, 1959) reported that snails migrated in "schools". Yet the life history of this species (in particular, the far-flung dispersal of larvae (Scheltema, 1971) and the genetic similarities of populations along the western Atlantic coast (Gooch et al., 1972)) suggested loose kinship among individuals on a flat. Thus, little social interaction should be expected (Wilson, 1975).

The results of the brief study reported here suggest that the "schools" are temporary and are not maintained by interactions between individuals.

The work was done in the intertidal zone in part of the Jamaica Bay and Raunt Wildlife Park, Gateway National Park, Brooklyn, New York. No visitors are permitted on this beach, so the snails were not disturbed during the study. Observations were made from October 23 to November 10, 1974. After November 10, there were only a few snails left in the intertidal zone.

Four 0.34 m^2 quadrats were placed on the flat in the center of four different and distinct aggregations of snails located at different tide marks on the flat. The total number of snails in each quadrat was counted, including those which were buried (none deeper than the black reducing layer) (Table 1). On October 23, the shells of 50 snails from each of two quadrats, both at mean low tide (MLT a and MLT b) were marked with different colors of model airplane glue. On October 25 all the snails from one quadrat at the mean tide mark (MT) and on October 26 all the snails from a quadrat at the mean high tide mark (MHT) were marked. After marking, all snails were returned to the quadrat from which they were removed.

TABLE 1. Number of individuals found in each quadrat on the date of marking and on the last observation day.

Date	QUADRAT							
	Mean Low Tide a		Mean Low Tide b		Mean Tide		Mean High Tide	
	number	number/m	number	number/m	number	number/m	number	number/m
Oct. 23/74	148	1113.7	235	1768.4				
Oct. 25/74					168	323.6		
Oct. 26/74							65	489.1
Nov. 21/74	0	0	9	67.7	43	344.0	0	0

Observations were made at low tide and consisted of measuring: 1) the distance of each marked individual from the central point of the quadrat where it was found, and 2) the position of each marked individual in polar coordinates relative to the central point of the quadrat where it was found. O° was taken as magnetic West-Northwest, and the edge of the water at low tide was taken as 90°. Observations were made on four days between October 23 and November 21, 1974.

Individuals of a specific aggregation did not remain at a specific site. Marked snails were found farther away from their release point through time. The regression of distance against time was significant for all quadrats (MHT, $F_{(1,75)} = 10.35$; MLT a, $F_{(1,75)} = 27.97$; MLT b, $F_{(1,65)} = 11.18$; MT, $F_{(1,125)} = 36.71$. All p's $< .01$).

Further, individuals of a specific aggregation did not remain together for relatively long periods of time. Relative distances between adjacent snails are a good measure of aggregation; distances between two snails in the same aggregation will generally be shorter than distances between two snails in two different aggregations. Further, one would expect the former distances to remain fairly constant through time if the same snails remained together as members of a real "school". On the other hand, if the distances between individuals in the group increased with time then one might conclude that the aggregation was not permanent, but a temporary grouping of individuals which moved apart, and whose members became members of other, new aggregations.

The location of snails from each original quadrat on each day were plotted on polar coordinate paper. The distance from each snail to its nearest neighbor from that original quadrat was measured in millimeters. The data were then treated as were the distances from point of release. At all stations the regression of distance between snails against time was significant (MHT, $F_{(1,75)} = 4.07$; MLT a, $F_{(1,75)} = 41.67$; MLT b, $F_{(1,65)} = 20.63$; MT, $F_{(1,125)} = 7.07$. All p's $< .05$). The rate of disaggregation of the snails at the mean and mean high tide mark was lower than the rate at the mean low tide mark.

Not only were the snails moving away from each other, but they were moving away in random directions. Pielou (1969) calculated that, in a random dispersion, 0.6215 of the individuals will have the same nearest neighbor as its nearest neighbor – in other words, that two individuals will be closer to each other than to any other snail. The Chi Square Test was used to determine whether the number of observed mutual pairs was what would be expected if the marked snails were randomly dispersed relative to each other, for each station for each observation day. In all cases, the number of observed mutual pairs was not significantly different from the number that was expected. Thus, members of the original aggregations disaggregated, separating further from each other with time, and taking random walks relative to each other.

It may be concluded that the aggregations studied were not social units. Perhaps they were the result of the snails' attraction to the same site on the flat caused by chemical stimuli (Carr, 1967; Crisp, 1969; Gurin & Carr, 1971), or what would be expected in a random dispersion. Further, the snails showed no permanent affinity for a particular place on the flat; they tended to be found more distant from their original site with each observation day. Finally, the movements of the snails were essentially random walks.

I thank J. Tietjen for critical reading of the manuscript and K.O. Morgan for permission to do the field work in the bird sanctuary at Jamaica Bay, Gateway National Recreation Area.

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BETTY BOROWSKY, *Osborn Laboratories of Marine Sciences, Boardwalk West 8th Street, Brooklyn, New York 11224, U.S.A.*

A NEW RANGE EXTENSION OF *BIOMPHALARIA ALEXANDRINA*, THE SNAIL INTERMEDIATE HOST OF *SCHISTOSOMA MANSONI* IN EGYPT.[1] – Schistosomiasis has been recognized as an endemic public health problem in Egypt since the advent of recorded medical history. Medical papyri of the pharonic era almost 4,000 years old describe the symptomatic hematuria found in acute cases of urinary schistosomiasis, and recently performed autopsies of the mummified remains of ancient inhabitants of the Nile Valley give positive evidence of the presence of the disease (Ruffer, 1910), which was no doubt well established in prehistory.

Bilharz (1852), working in Cairo, first attributed the causative agency of the disease to the digenetic trematode *Schistosoma haematobium* (Bilharz), which at that time was the prevalent schistosome species throughout the country. *S. mansoni* Sambon, the parasitic agent of intestinal schistosomiasis, is also endemic to Egypt, but its principle distribution is restricted to the region around Cairo and the Nile River delta. The disease is occasionally encountered allochthonously south of this area. This disease resumes its southern distribution near Khartoum in the Sudan, leaving a 1,600 km expanse of the Nile Valley free from transmission foci.

Schistosoma haematobium, endemic throughout the Nile basin, shows an epidemiological pattern well correlated with the zoogeographic distribution of the snail intermediate host, *Bulinus truncatus* (Audouin), and concomitant human settlements. Autochthonous *S. mansoni* infections are similarly distributed in relation to the occurrence of its respective hosts, *Biomphalaria alexandrina alexandrina* (Ehrenberg) in Egypt and *Bi. pfeifferi* (Krauss) in the northern Sudan (Omer, 1978).

Biomphalaria alexandrina in Egypt was reported to be confined to the vicinity of Cairo and the delta by Jordan & Webbe (1969) and El Alamy & Cline (1977). However, Abdel Malek (1958) cited evidence of a slightly more southerly limit of the range to Fayoum oasis and Beni Suef Governorate, 100 km south of Cairo.

Methods. Snail surveys were conducted at several sites in Aswan Governorate during January 1978, June 1978, January 1979 and May 1979 as part of our continuing survey of the genus *Bulinus* in Egypt, for the purpose of determining the distribution of snail intermediate hosts of schistosomiasis. Various collection techniques were employed as appropriate to sampling conditions and included use of standard 30 cm x 30 cm wire mesh snail scoops, hand harvesting of vegetation, and Ekman and Petersen bottom dredges. All snail specimens encountered were collected, measured and recorded. Six sites were arbitrarily chosen during the 1978 surveys to provide a variety of habitat types. Sites selected in the two 1979 surveys were selected after consideration of the 1978 results and after January communications with the Aswan Governorate Ministry of Health, from which it was learned that attempts had been made to eradicate a small population of *Biomphalaria* along a 50 m stretch of the Nile waterfront in the city.

Results. *Bulinus truncatus* was present at each of the six sites sampled in the city of Aswan during the 1978 surveys; no *Biomphalaria* were encountered. During January 1979, *Bu. truncatus* also was found at all sites and, additionally, 56 *Bi. alexandrina* were recovered after a 5 man-hour search of the Nile corniche. Subsequent surveys conducted north of the city of Aswan yielded three specimens after a 1.5 man-hour search effort. At Khatara, 15 km north of the city, two individuals were recovered after 0.75 man-hours of search, and three specimens were taken in a 6 man-hour search of the Nile at Iqlit, 45 km north of Aswan.

In May 1979, a brief survey of three sites along the corniche in Aswan was conducted to determine the status of *Biomphalaria alexandrina* in the region; 54 specimens were recovered in 2.3 man-hours. A 2 man-hour search of the River Nile at Sebaie, 140 km north of Aswan, resulted in collection of large quantities of *Bulinus*. However, no *Biomphalaria* were found. Similarly, a 4 man-hour search of the river at the village of Roffa, 10 km south of Luxor, failed to give evidence of the presence of *Biomphalaria* although *Bulinus* was in abundance.

Discussion. The historical trend in schistosomiasis vector snail dispersal in the Nile Valley over the past 70 years has been characterized by gradual increases in distribution and abundance of both vector species, presumably in response to environmental alterations resulting from man-made hydrological changes in river discharge and altered irrigation practices. *Biomphalaria alexandrina* was originally restricted to the coastal delta and slowly invaded southward, usually first appearing in stagnant swamps and pools or slowly flowing drainage canals (Gismann, pers. comm.). El Alamy & Cline (1977) reported a notable increase in abundance of *Biomphalaria* over the last decade in the southeastern delta region. In Gezira project in the Sudan, Omer (1978) reported a similar steady increase in *Bi. pfeifferi* over the past 25 years, with a concomitant increase in *Schistosoma mansoni* in the irrigated area.

The unanticipated and sudden appearance of a breeding population of *Biomphalaria alexandrina* over a 45 km reach of the Nile in Aswan, the southern-most governorate in Egypt, indicates a significant dispersal from the formerly reported limits of distribution. This recent extension is not in keeping with the slow dispersal patterns previously noted. Although there are many widely recognized agencies for spread of snail vectors (which may include drift, rafting, dispersal by migrating birds and transport in mud caked upon bodies and within hoofs of ungulates, as well as in water transported by man for drinking and irrigation), the circumstances of the present situation may be more likely attributable to the increasing number of motor vessels which ply the river between Cairo and Aswan for commerce and tourism, a journey which

commonly is made in six days. Although the transport of adult snails on the undersides of the vessels is highly unlikely, attached egg masses may remain in place and could liberate young at the southern terminus. The location of the most dense populations along the Aswan corniche is consistent with this hypothesis. The decreasing, less dense nature of the downstream populations may indicate that the vessel docking area in the city of Aswan is serving as dispersal point for the dissemination of the Upper Egyptian population by passive downstream drift. Although we may only speculate on the actual agency of introduction, the establishment and spread of *B. alexandrina* in the region has been made possible as a result of river ecology modifications, resulting from the effects of the Aswan High Dam construction.

The future human health impact of this situation is considerable. The present conditions have demonstrated that introduction and establishment of the snail intermediate host of *Schistosoma mansoni* in Upper Egypt has been accomplished under the new environmental conditions resulting from the construction of the High Dam, and further increases in *Biomphalaria alexandrina* can be expected throughout the country. The probability of establishing transmission of the disease throughout the Nile Valley is now very high. Allochthonous cases of intestinal schistosomiasis have been observed recently by Miller (pers. comm.) near Aswan (in rural villagers who had spent time in the delta) and by King (unpubl. data) in the Luxor vicinity. In consideration of the history of establishment of the disease in areas previously free of transmission, it is possible that millions of rural Egyptians inhabiting the Nile Valley between Aswan and Cairo will be exposed to dual infections of intestinal and urinary schistosomiasis over the next decades.

Acknowledgements. The authors wish to express their appreciation to Eng. Mahmoud Gaber for arrangements of field collecting trips and to Dr. Emile S. Demian for positive identification of *Biomphalaria alexandrina alexandrina*. Special thanks are due to Ali Hassan, J. Bailey, V. Demers, J. Graves, A. El Sayed, S. McMahon and M. Nagi for assistance in collection.

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JOHN C. MALLETT, *Department of Biological Sciences, University of Lowell, Lowell, Massachusetts 01854, U.S.A.*

IBRAHIM A. ABOUL-ELA, *Department of Zoology, Ain Shams University, Cairo, A. R. Egypt*

(1)This work was supported by grants from the United States Department of Health, Education and Welfare (National Institutes of Health, Public Law 480 Agreement 03-044N), and the Smithsonian Institution (FC809483), Washington, D.C., U.S.A. Voucher specimens have been deposited in the Museum of Zoology, The University of Michigan, Ann Arbor, Michigan, U.S.A.

SOME RECENT COLLECTIONS OF MUSSELS FROM SOUTHEASTERN MICHIGAN. – This report concerns some recent collections of mussels in the Lake Erie drainage of southeastern Michigan. Other recent records from this area are reported in van der Schalie (1970), Clarke (1973) and Clark (1977). For earlier records, see Goodrich (1932), van der Schalie (1938), and references cited in those two publications.

The streams in the study area are low gradient hardwater streams (Knutilla & Allen, 1975). Most of the streams examined are less than 20 m wide, and all are shallow (<1½ m in low water stages). Bottom types range from bedrock and cobbles to silt and clay, although sandy substrata predominate. Macrophytes are generally rare or absent.

All watersheds in this area have been greatly altered from their natural states. Land use is predominantly agricultural and urban, resulting in loads of silt, agricultural chemicals, and domestic and industrial wastes to the streams. All river systems have numerous dams, which probably act as significant barriers to fish dispersal and convert free-flowing stretches to ponded backwaters as well.

Collections were made at 26 stations (see Fig. 1) in 1976-78. Handpicking was employed, sometimes augmented by use of a garden rake or a ½"-mesh wire screen (which was particularly useful in recovering small shells). Live mussels were identified and representative shells of most species were saved.

The results (see Table 1) show relative abundances in terms of the number of live specimens that I was able to collect per hour during a period of optimal conditions. They should not be taken as quantitative, but rather as rough indices of abundance. All species have been reported previously from the State of Michigan.

Carunculina glans, Simpsoniconcha ambigua, Lasmigona complanata and *Anodonta imbecilis* (?, see Table 1) are new records for the Raisin drainage (cf. van der Schalie, 1938, and records of the Museum of Zoology, The University of Michigan [UMMZ]). The first two are of rare and spotty occurrence in Michigan, and are part of the lower Macon Creek fauna (Station 8), which comprised 18 species, including three (*C. glans, S. ambigua* and *Dysnomia torulosa rangiana*) regarded by Stansbery (1970) as endangered. The latter two may be recent invaders to the lower Raisin, along with *Carunculina parva*, which is new to the lower river (UMMZ records). Van der Schalie (1938) reported that *L. complanata* had apparently invaded the Huron River in historical times, and, along with *C. parva*, dominated impounded stretches of that river.

Many stations, particularly in the headwaters, still contain healthy mussel populations. For these places, my species lists compare very favorably with previous records (Stations 1 and 2 with Clark's (1977)

FIG. 1. Map of collecting localities in this study. Locality numbers are the same as given in Table 1.

TABLE 1. Distribution and abundance of mussels found in southeastern Michigan.

Localities[1]	Species																													
	A. costata	*C. tuberculata*	*E. dilatata*	*F. flava*	*P. clava*	*P. c. coccineum*	*A. calceolus*	*A. marginata*	*A. grandis*	*A. imbecilis*	*A. fetussacianus*	*L. complanata*	*L. compressa*	*L. costata*	*S. ambigua*	*S. undulatus*	*A. carinata*	*C. glens*	*C. parva*	*D. t. rangiana*	*D. triquetra*	*L. fasciola*	*L. r. stiliquoidea*	*L. o. ventricosa*	*L. recta*	*V. fabalis*	*V. iris*	*P. fasciolare*
1. St. Josephs R. (of Maumee drainage), E. Fork of W. Br., Cambria Rd., Hillsdale Co.	C		A	C	C	R	C	D						D			D					C	R	C			A	A
2. St. Josephs R. (of Maumee drainage), W. Fork of W. Br., Territorial Rd., Hillsdale Co.	R		A	C		D	R	R	D				D			R						C	R				A	D
3. Bean Cr., 1-2 km below Dillon Hgwy., Lenewee Co.	R		C	R		R	D	R	D		R	R	R	R		C							C	A			R	
4. R. Raisin, Monroe St., Monroe, Monroe Co.		D				D			A			C		D			D		R			D	A				D	
5. R. Raisin, Telegraph Rd., Monroe, Monroe Co.		D	D	D					A	D?							D		D				A	D		D		D
6. R. Raisin, Raisinville Rd., Monroe Co.	D	D	D	D					A								D						C	D			D	D
7. R. Raisin, Doty Rd., Monroe Co.	D	D	D	D					C								D						C	D				
8. Macon Cr., Stowell Rd., Monroe Co.	D	D	D	D		D	D		D		D				D	D	D	D		D			D		D	D	D	D
9. Macon Cr., Dundee-Azalia Rd., Monroe Co.	D			C		D	D				D												A					
10. Macon Cr., N. Br., Day Rd., Monroe Co.									D		D																	
11. Macon Cr., Mid. Br., Wilcox Rd., Monroe Co.	C			D							D												A					
12. Macon Cr., Mid. Br., Petersburg Rd., Monroe Co.				D			C				C		C										A					
13. Macon Cr., S. Br., Wilcox Rd., Monroe Co.	A			C			C		D		D*												A					
14. Macon Cr., S. Br., Petersburg Rd., Monroe Co.	A			C			R		R		D*		C			D							A					
15. Wolf Cr., Tipton Hgwy., Adrian, Lenewee Co.							R				R												A					
16. Evans Cr., Maumee St., Tecumseh, Lenewee Co.																												
17. R. Raisin, Evans St., Tecumseh, Lenewee Co.								C	D														A	C				
18. R. Raisin, Staib Rd., Lenewee Co.			D	R				C	D				C			D						R	A	C			D	
19. R. Raisin, Austin Rd., Manchester, Washtenaw Co.		D	D	D			D	D					D			D							D	D			D	
20. R. Raisin, Sharon Valley Rd., downstream crossing, Washtenaw Co.		C	C	C		C	D						C			R						C	C	A			C	
21. R. Raisin, Sharon Valley Rd., upstream crossing, Washtenaw Co.		R	R	C		R			D				D										D*		C			D*	
22. Goose Cr., Cement City Hgwy., Lenewee Co.																													
23. Sandy Cr., Dixie Hgwy., Monroe Co.																													
24. Stony Cr., Telegraph Rd., Monroe Co.				D												D							C	D			D	
25. Huron R., Argo Dam to Gallup Park, Ann Arbor, Washtenaw Co.		R	D					D	R	D*			R			R			D					C			D	
26. Portage R., NE of Silver Lk., Washtenaw Co.			C					R	R				R			R					R	C	R	A			C	A

A = abundant, >5 specimens/man-hour; C = common, 1-5 specimens/man-hour; R = rare, <1 specimen/man-hour; D = only dead shells found; D* = presumed to be living at site, but no live specimens seen; ? = specimen lost.

[1]Locality numbers correspond to numbers on the map in Fig. 1.

1948 work; Station 26 with van der Schalie's (1938) 1932 results; others with UMMZ records between the years 1880 and 1930). Thus, it seems that these streams have retained their original faunas.

In contrast, the lower river faunas appear to have been greatly reduced, probably due to domestic and industrial wastes. For example, the lower Raisin (Stations 4-7), which now contains four species, once held 20 (UMMZ records). But, even here, mussel density of those four species is fairly high today, and so, in spite of past history, current conditions are favorable for mussels. I believe what has happened here (and this may apply elsewhere as well) is that the original fauna was destroyed by pollution, but the river was recolonized once conditions again became suitable. A balance between periodic local extinction or depletion and recolonization might then occur. Where such conditions exist, we might expect species composition to shift towards good colonizers; species possessing such traits as rapid growth, early maturity, numerous or mobile fish hosts, and tolerance to many substrata, as well as resistance to the specific factors causing mortality. It is interesting to note that, of the four species now in the lower Raisin, two (*Lampsilis radiata siliquoidea* and *Anodonta grandis*) have many reported fish hosts (Fuller, 1974), and available data (Coker et al., 1922) suggest that all four grow rapidly and mature quickly. If water quality remains good, they might be joined by slower colonizers, and an extensive fauna might develop, depending upon the frequency of bouts with pollution. Because mussels have long life histories and rather exacting habitat requirements (e.g., see van der Schalie, 1938), colonization may be slow (especially in drainages with barriers like dams, waterfalls, or lakes), and even rare episodes of pollution may be sufficient to greatly affect faunal composition.

Acknowledgements. I am grateful to J. Bondus, R. Hanley, G. Likens, C. Drumm, M. Strayer, the Michigan Nature Association, and especially H. van der Schalie, for their generous help in this work.

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DAVE STRAYER, *Department of Ecology and Systematics, Cornell University, Ithaca, New York 14853, U.S.A.*

FRESHWATER MOLLUSK FAUNA OF THE KHUZESTAN AND KHORRAM-ABAD AREAS IN SOUTHWESTERN IRAN. – The Khuzestan and Khorram-abad areas are located in the tropical and subtropical regions of southwestern Iran. These areas have a good variety of aquatic snails and, compared to other parts of Iran, a high incidence of snail-borne trematode infections in man and other mammals. The snails recorded below were collected in various water bodies in the areas. After being relaxed in a menthol solution, the snails were preserved in 70% alcohol. The identifications of the snail species were based on shell characters, as well as on the morphology of internal organs. Preserved specimens were sent to the Danish Bilharziasis Laboratory (World Health Organization Snail Identification Centre) at Charlottenlund, Denmark, for confirmation of identifications. Voucher specimens have been deposited in the collections of the Danish Bilharziasis Laboratory.

The species of aquatic mollusks found in the Khuzestan area were *Bulinus truncatus* (Audouin), *Gyraulus intermixtus* (Mousson), *G. euphraticus* (Mousson), *Lymnaea (Radix) auricularia* Linnaeus (form *gedrosiana* Annandale & Prashad), *L. (Fossaria) truncatula* (Müller), *Physa acuta* Draparnaud, *Melanoides tuberculata* (Müller), *Melanopsis costata* (Férussac), *M. praerosa* (Linnaeus), *M. nodesa* (Férussac), *Viviparus bengalensis* (Lamarck), *Corbicula fluviatilis* (Müller), *Theodoxus euphraticus* (Mousson), *T. cinctellus* (Martens) and *Unio* sp.

The species of aquatic mollusks found in the Khorram-abad area were *Gyraulus convexiusculus* (Hutton), *Melanopsis buccinoides* (Mousson), *Theodoxus doriae* (Issel), *Bithynia rubens* (Martens), *Physa acuta*, *Lymnaea (Radix) auricularia*, *L. (Fossaria) truncatula* and *Pisidium nitidum* Jenyns.

In respect to snail-borne trematode infections in the area, Table 1 shows the intermediate and final hosts of some of these parasites.

TABLE 1. Mammalian trematode parasites and their intermediate and final hosts in the Khuzestan and Khorram-abad areas.

No.	Parasite	Intermediate host	Final host
1	*Schistosoma haematobium*	*Bulinus truncatus*	Man
2	*Schistosoma bovis*	*Bulinus truncatus*	Ruminants
3	*Ornithobilharzia turkestanicum*	*Lymnaea auricularia*	Ruminants
4	*Fasciola hepatica*	*Lymnaea truncatula*	Ruminants
5	*Fasciola gigantica*	*Lymnaea auricularia*	Ruminants
6	*Paramphistomum micyobothrium*	*Bulinus truncatus*	Ruminants
7	*Gymnocephalus* sp.	*Lymnaea auricularia* *Gyraulus* sp.	Unknown
8	*Heterophyes* sp.	Unknown	Man & carnivores
9	*Metagonimus* sp.	Unknown	Man & carnivores
10	*Opisthorchis* sp.	Unknown	Pig
11	*Alaria alariae*	Unknown	Carnivores
12	Bird schistosomes	Unknown	Aquatic birds

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J. MASSOUD and M. HEDAYETI-FAR, *School of Public Health and Institute of Public Health Research, P. O. Box 1310, Teheran University, Teheran, Iran.*

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GENERA AND SUBGENERA OF RECENT FRESHWATER GASTROPODS OF NORTH AMERICA (NORTH OF MEXICO)*

Subclass PROSOBRANCHIA

NERITINIDAE Rafinesque 1815
- *Neritina* Lamarck 1816 (*Nerita pulligera* Linnaeus 1766)**
  - *Vitta* Mörch 1852 (*Nerita virginea* Linnaeus 1758)

VALVATIDAE Gray 1840
- *Valvata* Müller 1774 (*Valvata cristata* Müller 1774)

VIVIPARIDAE Gray 1847
- Viviparinae s.s.
  - *Tulotoma* Haldeman 1840 (*Paludina magnifica* Conrad 1834)
  - *Viviparus* Montfort 1810 (*Helix vivipara* Linneaus 1758)
- Bellamyinae Röhrbach 1937
  - †*Cipangopaludina* Hannibal 1912 (*Paludina malleata* Reeve 1862)
- Lioplacinae Gill 1863
  - *Campeloma* Rafinesque 1819 (*Campeloma crassula* Rafinesque 1819)
  - *Lioplax* Troschel 1856 (*Limnaea subcarinata* Say 1817)

AMPULLARIIDAE Guilding 1828
- †*Marisa* Gray 1824 (*Helix cornuarietis* Linnaeus 1758)
- *Pomacea* Perry 1810 (*Pomacea maculata* Perry 1810)

MICROMELANIIDAE Thiele 1928
- *Antroselates* Hubricht 1963 (*Antroselates spiralis* Hubricht 1963)

HYDROBIIDAE Troschel 1857††
- Hydrobiinae s.s.
  - *Aphaostracon* Thompson 1968 (*Aphaostracon rhadinus* Thompson 1968)
  - *Hoyia* F. C. Baker 1926 (*Amnicola sheldoni* Pilsbry 1890)
  - *Hyalopyrgus* Thompson 1968 (*Bythinella aequicostata* Pilsbry 1889)
  - *Littoridinops* Pilsbry 1952 (*Amnicola tenuipes* Couper (in Haldeman) 1844)
  - *Probythinella* Thiele 1928 (*Paludina emarginata* Küster 1852 = *Probythinella lacustris limafodens* Morrison 1947)
  - *Pyrgophorus* Ancey 1888 (*Pyrgulopsis spinosus* Call & Pilsbry 1886)
  - *Tryonia* Stimpson 1865 (*Tryonia clathrata* Stimpson 1865)
- Lithoglyphinae Troschel 1857
  - *Antrobia* Hubricht 1971 (*Antrobia culveri* Hubricht 1971)
  - *Clappia* Walker 1909 (*Clappia clappi* Walker 1909 = *Somatogyrus umbilicatus* Walker 1904)
  - *Cochliopina* Morrison 1946 (*Cochliopa riograndensis* Pilsbry & Ferriss 1906)
  - *Fluminicola* Stimpson 1865 (*Paludina nuttalliana* Lea 1838)
  - *Gillia* Stimpson 1865 (*Melania altilis* Lea 1842)
  - *Lepyrium* Dall 1896 (*Neritina showalteri* Lea 1861)
  - *Somatogyrus* Gill 1863
    - *Somatogyrus* s.s. (*Amnicola depressa* Tryon 1862)
    - *Walkerilla* Thiele 1928 (*Somatogyrus coosaensis* Walker 1904)

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*Modified from *Journal de Conchyliologie*, 1978, Vol. CXV, Nos 1 et 2, p 3-9.

**Type species are placed in parentheses after each generic-group name.

†Recent introduction to North America.

††The subfamilial arrangement for the Hydrobiidae is a provisional one.

Nymphophilinae Taylor 1966
Birgella F. C. Baker 1926 (*Paludina subglobosa* Say 1825)
Cincinnatia Pilsbry 1891 (*Paludina cincinnatiensis* Anthony 1841)
Fontelicella Gregg & Taylor 1965
Fontelicella s.s. (*Fontelicella californiensis* Gregg & Taylor 1965)
Natricola Gregg & Taylor 1965 (*Pomatiopsis robusta* Walker 1908)
Microamnicola Gregg & Taylor 1965 (*Amnicola micrococcus* Pilsbry (in Stearns) 1893)
Marstonia F. C. Baker 1926 (*Amnicola lustrica* Pilsbry 1890)
Notogillia Pilsbry 1953 (*Hydrobia wetherbyi* Dall 1885)
Orygoceras Brusina 1882 (*Orygoceras cornucopiae* Brusina 1882)
Pyrgulopsis Call & Pilsbry 1886 (*Pyrgula nevadensis* Stearns 1883)
Rhapinema Thompson 1969 (*Rhapinema dacryon* Thompson 1969)
Spilochlamys Thompson 1968 (*Spilochlamys conica* Thompson 1968)
Stiobia Thompson 1978 (*Stiobia nana* Thompson 1978)
Amnicolinae Tryon 1862
Amnicola Gould & Haldeman 1840
Amnicola s.s. (*Paludina porata* Say 1821 = *Paludina limosa* Say 1817)
Lyogyrus Gill 1863 (*Valvata pupoidea* Gould 1841)
?*Hauffenia* Pollonera 1898 (*Horatia tellini* Pollonera 1898)
?*Horatia* Bourguignat 1887 (*Horatia klecakiana* Bourguignat 1887)
Fontigentinae Taylor 1966
Fontigens Pilsbry 1933 (*Paludina nickliniana* Lea 1838)

POMATIOPSIDAE Stimpson 1865
Pomatiopsis Tryon 1862 (*Cyclostoma lapidaria* Say 1817)

BITHYNIIDAE Gray 1857
Bithynia Leach (in Abel) 1818 (*Helix tentaculata* Linnaeus 1758)

THIARIDAE Troschel 1857
†*Melanoides* Olivier 1804 (*Nerita tuberculata* Müller 1774)
†*Thiara* Röding 1798 (*Helix amarula* Linnaeus 1758)

PALUDOMIDAE Gill 1871 (STREPOMATIDAE Haldeman 1863, PLEUROCERIDAE Fischer 1885)§
Elimia H. & A. Adams 1854 (*Melania acutocarinata* Lea 1841 = *Melania clavaeformis* Lea 1841) [synonyms: *Goniobasis, Macrolimen, Melasma*]
Gyrotoma Shuttleworth 1845 (*Gyrotoma ovoidea* Shuttleworth 1845 = *Melania excisa* Lea 1843) [synonym: *Apella*]
Io Lea 1831 (*Fusus fluvialis* Say 1825) [synonym: *Melafusus*]
Juga H. & A. Adams 1854
Juga s.s. (*Melania silicula* Gould 1847)
Calibasis Taylor 1966 (*Melania* (?*Goniobasis*) *acutifilosa* Stearns 1890)
Oreobasis Taylor 1966 (*Melania newberryi* Lea 1860 = ?*Melania bulbosa* Gould 1847)
Leptoxis Rafinesque 1819 (*Melania praerosa* Say 1821) [synonyms: *Anaplocamus, Anculosa*]
Mudalia Haldeman 1840 (*Paludina dissimilis* Say 1819 = *Bulimus carinatus* Bruguière 1792) [synonyms: *Alleghenya, Spirodon*]
Lithasia Haldeman 1840 (*Anculosa (Lithasia) geniculata* Haldeman 1840) [synonyms: *Angitrema, Athearnia, Eurycaelon, Glottella, Megara, Meseschiza*]

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† Recent introduction to North America.

§A critical revision of the Paludomidae has not yet been made. The generic groups listed here are based on classical shell characters, even though it is realized that these characters mostly seem to intergrade at one point or another. Animal characteristics of value in paludomid systematics are currently so incompletely known that they cannot be used to precisely characterize biological generic groups or to assign the great majority of species to definite nomenclatural generic groups. *Pleurocera* is used as though *P. acuta* were its type species in the expectation that the International Commission on Zoological Nomenclature will adopt the long-standing petition to preserve this usage. The identity of *Ellipstoma gibbosa* Rafinesque 1818 is too doubtful to give nomenclatural validity to *Ellipstoma* Rafinesque 1818.

Pleurocera Rafinesque 1818 (*Pleurocera acuta* Rafinesque 1831) [synonyms: *Ceriphasia, Oxytrema, Strepoma, Telescopella, Trypanostoma*]
Strephobasis Lea 1861 (*Strephobasis cornea* Lea 1861 = *Melania plena* Anthony 1854)

Subclass PULMONATA

ACROLOXIDAE Thiele 1931
Acroloxus Beck 1837 (*Patella lacustris* Linnaeus 1758)

LYMNAEIDAE Rafinesque 1815
Acella Haldeman 1841 (*Lymnaea gracilis* Jay 1839, preocc. = *Limnaea haldemani* "Deshayes" W. G. Binney 1867)
Bulimnea Haldeman 1841 (*Lymnaeus megasomus* Say 1824)
Fossaria Westerlund 1885
Fossaria s.s. (*Buccinum truncatulum* Müller 1774)
Bakerilymnaea Weyrauch 1964 (*Limnaea cubensis* Pfeiffer 1839)
Lymnaea Lamarck 1799 (*Helix stagnalis* Linnaeus 1748)
Pseudosuccinea F. C. Baker 1908 (*Lymnaea columella* Say 1817)
†*Radix* Montfort 1810 (*Radix auriculatus* Montfort 1810 = *Helix auricularia* Linnaeus 1758)
Stagnicola Leach (in Jeffreys) 1830
Stagnicola s.s. (*Buccinum palustre* Müller 1774)
Hinkleyia F. C. Baker 1928 (*Lymnaeus caperatus* Say 1829)
Lanx Clessin 1882
Lanx s.s. (*Ancylus newberryi* Lea 1858 = *Ancylus patelloides* Lea 1856)
Walkerola Hannibal 1919 (*Lanx (Walkerola) klamathensis* Hannibal 1912)
Fisherola Hannibal 1912 (*Fisherola lancides* Hannibal 1912)

PHYSIDAE Fitzinger 1833
Physinae s.s.
Physa Draparnaud 1801 (*Bulla fontinalis* Linnaeus 1758)
Physella Haldeman 1843
Physella s.s. (*Physa globosa* Haldeman 1841)
Costatella Dall 1870 (*Physa costata* Newcomb 1861)
Petrophysa Pilsbry 1926 (*Physa (Petrophysa) zionis* Pilsbry 1926)
Aplexinae Starobogatov 1967
Aplexa Fleming 1820 (*Bulla hypnorum* Linnaeus 1758)
Stenophysa Martens 1898 (*Physa sowerbyana* d'Orbigny 1853)

PLANORBIDAE Rafinesque 1815
Planorbinae s.s.
Planorbini s.s.
Gyraulus "Agassiz" Charpentier 1837
Gyraulus s.s. (*Planorbis hispidus* Draparnaud 1805 = *Planorbis albus* Müller 1774)
Armiger Hartmann 1840 (*Planorbis cristatus* Draparnaud 1805 = *Nautilus crista* Linnaeus 1758)
Torquis Dall 1905 (*Planorbis parvus* Say 1817)
Drepanotremini Zilch 1959 (?Acrorbini Starobogatov 1958)
Antillorbis Harry & Hubendick 1964 (*Planorbis circumlineatus* Shuttleworth 1854 = *Planorbis aeruginosus* Morelet 1851)
Drepanotrema Fischer & Crosse 1880 (*Planorbis ysabelensis* Crosse & Fischer 1879 = *Planorbis anatinus* d'Orbigny 1835)
Fossulorbis Pilsbry 1934 (*Planorbis cultratus* d'Orbigny 1841 = *Planorbis kermatoides* d'Orbigny 1835)
Biomphalariini Watson 1954
Biomphalaria Preston 1910 (*Biomphalaria smithi* Preston 1910)

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† Recent introduction to North America.

Helisomini F. C. Baker 1928
Helisoma Swainson 1840
Helisoma s.s. (*Planorbis bicarinatus* Say 1817, preocc. = *Planorbis anceps* Menke 1830)
Carinifex W. G. Binney 1865 (*Planorbis newberryi* Lea 1858)
Menetus H. & A. Adams 1855
Menetus s.s. (*Planorbis opercularis* Gould 1847)
Micromenetus F. C. Baker 1945 (*Planorbis dilatatus* Gould 1841)
Planorbella Haldeman 1842
Planorbella s.s. (*Planorbis campanulatus* Say 1821)
Pierosoma Dall 1905 (*Planorbis trivolvis* Say 1817)
Seminolina Pilsbry 1934 (*Paludina scalaris* Jay 1839)
Planorbula Haldeman 1840 (*Planorbis armigerus* Say 1821)
Promenetus F. C. Baker 1935 (*Planorbis exacuous* Say 1821)
Vorticifex Meek (in Dall) 1870
Vorticifex s.s. (*Carinifex (Vorticifex) tryoni* Meek (in Dall) 1870)
Parapholyx Hanna 1922 (*Pompholyx effusa* Lea 1856)
Neoplanorbinae Hannibal 1912
Amphigyra Pilsbry 1906 (*Amphigyra alabamensis* Pilsbry 1906)
Neoplanorbis Pilsbry 1906 (*Neoplanorbis tantillus* Pilsbry 1906)

ANCYLIDAE Rafinesque 1815
Ancylinae s.s.
Rhodacmea Walker 1917
Rhodacmea s.s. (*Ancylus filosus* Conrad 1834)
Rhodocephala Walker 1917 (*Rhodacmea (Rhodocephala) rhodacme* Walker 1917)
Ferrissinae Walker 1917
Ferrissia Walker 1903 (*Ancylus rivularis* Say 1817)
Laevapicinae Hannibal 1912
Hebetancylus Pilsbry 1914 (*Ancylus moricandi* d'Orbigny 1836)
Laevapex Walker 1903 (*Ancylus fuscus* C. B. Adams 1841)

J. B. BURCH

Museum of Zoology and Department of Ecology and Evolutionary Biology
The University of Michigan
Ann Arbor, Michigan 48109, U.S.A.

NEWS AND ANNOUNCEMENTS

* * * * *

NEW SCIENTIFIC JOURNAL – *MONOGRAPHS OF MARINE MOLLUSCA*. – A new serial publication on mollusks, *Monographs of Marine Mollusca*, has been announced by the Editor-in-Chief, Dr. R. Tucker Abbott. *Monographs of Marine Mollusca* is a professional journal devoted to the systematics, biology, zoogeography and taxonomy of marine mollusks, both living and fossil, and will deal with taxonomic revisions of the living and Tertiary marine Mollusca of the world. The journal will be issued with color plates and in a convenient looseleaf form compatible with the former *Indo-Pacific Mollusca*. Numbers will be issued irregularly as research is completed. Number 1 is "The Family Cerithiidae in the Indo-Pacific" by R.S. Houbrick of the Smithsonian Institution. Numbers in preparation include the Mitridae by W.O. Cernohorsky, *Babylonia* by Altena and Gittenberger, and others. Subscribers should contact the publisher, *American Malacologists, Inc.*, P.O. Box 4208, Greenville, Delaware 19807, U.S.A. The price of No. 1 is US$ 17.50 (or US$ 26.00, which includes a special looseleaf binder).

THE CONCHOLOGICAL SOCIETY OF GREAT BRITAIN AND IRELAND. – The program of the Society for the first half of 1979 included exhibitions by Mrs. K. Smythe on "Living mollusks of the Persian Gulf", Dr. R. Anderson on "Irish molluscs by an Irishman", Dr. J. Taylor on "Predatory gastropods", Mr. A.P.H. Oliver on "World wide chitons" and Mr. R.V. Melville on "The code of nomenclature and the I.C.Z.N. – how they serve the zoologist".

Exhibits for the latter half of 1979 will include "Non-marine fauna of Jamaica" by Dr. C.R.C. Paul on October 20, "The evolution of the cephalopods" by Prof. D.T. Donovan on November 17, and on December 15 an exhibition of Christmas cards, posters, advertizements, ornaments, toys, etc., using molluscs.

Meetings are held at 2:30 P.M. in the British Museum (Natural History), Cromwell Road, South Kensington SW7, London, England.

A SYMPOSIUM ON THE BIOLOGY AND ECOLOGY OF MOLLUSCA was held at The Australian Museum, Sydney, Australia, during the period May 21-25, 1979. The Symposium was organised by Dr. W.F. Ponder of The Australian Museum and Dr. A.J. Underwood of the University of Sydney, and was attended by 140 scientists, including students, from Australia, New Zealand, Hong Kong, Europe, Britain and the U.S.A. The papers dealt with a wide range of topics, but were mainly on the ecology of littoral marine molluscs and the evolution of molluscs. The abstracts of both the papers and posters will be published in the *Journal of the Malacological Society of Australia.*

PROGRAMME

Session 1. Chair: Dr. V. Fretter.
- B. Runnegar. Mollusca: the first hundred million years.
- K-J. Götting. Origin and relationships of the Mollusca.
- D.I. MacKinnon. New Zealand Middle Cambrian Mollusca: their nature and bearing on early molluscan evolution.
- J.H. McLean. Filter feeding aspidobranch limpets from submarine thermal springs on the Galapagos Rift - a new superfamily of archaic archaeogastropods.

Session 2. Chair: Dr. J.H. Choat.
- G.M. Branch. Territoriality in limpets: manipulative experiments and energy budgets.
- R.G. Creese. Patterns of vertical distribution of intertidal limpets in New South Wales.
- B. Morton. Selective site segregation in *Patelloida (Chiazacmea) pygmaea* and *P. lampanicola* on a Hong Kong shore.

Session 3. Chair: Dr. R.S. Houbrick.
- R. Black. Competition and stability in a guild of limpets.
- J.H. Choat & D.R. Schiel. The influence of grazing by subtidal gastropods on the establishment of fucoid algae.
- A.J. Underwood. The role of grazing by gastropods in the structure of intertidal communities.

Session 4. Chair: Dr. A. Solem.
- A.C. van Bruggen. Gondwanaland connections in the terrestrial molluscs of Africa and Australia.
- J. Walker. Comparative anatomy of *Bulinus* and *Isidorella*.
- M.J. Winterbourn. The distribution and biology of the freshwater gastropods, *Physa* and *Physastra* in New Zealand.

Session 5. Chair: Dr. F.E. Wells.
B.J. Smith. Relationships within the family Rhytididae.
A. Solem. Patterns of speciation in camaenid land snails of the Kimberley, Western Australia.
B. Miller. Experimental studies of the reproductive strategies of the intertidal limpet *Siphonaria kuracheensis*.
Session 6. Chair: Dr. R. Robertson.
C.S. Hickman. Functional interpretations of patterns in archaeogastropod radular morphology.
L.M. Joll. Aspects of the biology of *Octopus tetricus*.
A.H. Wären. Sexual strategies in Eulimidae (Prosobranchia).
Session 7. Chair: Dr. B. Runnegar.
C.M. Yonge. On the Plicatulidae and Dimyidae - proposed superfamily Plicatulacea.
R.G. Pearson. Aspects of the ecology of the giant clams *Tridacna giga* and *T. derasa*.
Session 8. Chair: Dr. W.B. Rudman.
R. Burn. The function of certain organs in the opisthobranch family Gastropteridae.
R. Hinde. Symbiotic chloroplasts in sacoglossans from south-eastern Australia.
M.C. Miller. Predator or prey: nudibranchs and coelenterates.
Session 9. Chair: Dr. M.C. Miller.
W.B. Rudman. Madreporarian coral and alcyonarian feeding by arminid and eolid opisthobranchs.
R. Rose. The zoogeography of some N.S.W. opisthobranchs in relation to their reproductive biology.
R.C. Willan. Ecology of sea hares (Aplysiidae) in the Leigh Marine Reserve, North Auckland, New Zealand.
Session 10. Chair: Prof. J.B. Burch.
F. Starmühlner. Freshwater gastropods of South Pacific islands.
W.F. Ponder. A remarkable hydrobiid fauna from Lord Howe Island (Gastropoda: Hydrobiidae).
D.W. Burton. Reproductive systems in the Athoracophoridae.
Session 11. Chair: Dr. B.J. Smith.
N. Coleman. The geography of littoral adaptation in bivalves.
P.N. Chalmer. Commensalism of the cap limpet, *Hipponix conicus*.
P. Huish. Factors influencing the distribution of *Conus* in East Australian waters.
Session 12. Chair: Sir C.M. Yonge.
V. Fretter. The evolution of higher taxa in gastropods.
J.D. Taylor. Food specialisation and the evolution of predatory gastropods.
F. Climo. A new order of interstitial, intertidal systellammatophoran slug from New Zealand, based on a new species and genus.
Session 13. Chair: Sir C.A. Fleming.
T.A. Darragh. Composition and origin of the molluscan fauna of the Tertiary of South Eastern Australia.
J.A. Grant-Mackie. Mode of life and adaptive evolution in the cosmopolitan Triassic bivalve *Monotis*.
R.S. Houbrick. Adaptive radiation in the Cerithiidae.
G.J. Vermeij. Scar tactics of gastropods: predation and the fossil record.
Session 14. Chair: Dr. J.D. Taylor.
A.J. Butler. Shore-level size-gradients in *Thais* spp.
M. Moran. Factors affecting feeding rates of the intertidal carnivorous gastropod *Morula marginalba*.
B.F. Phillips. A population model of the whelk *Thais orbita*.
Session 15. Chair: Dr. B.R. Wilson.
G. Parry. Life-history strategies of five species of intertidal limpet.
S.C. McKillup. Food related reproductive strategies in different populations of *Nassarius pauperatus*.
F.E. Wells. A quantitative examination of the benthic molluscs of Cockburn Sound, Western Australia.
Special Session on "The evolution of the Anomalodesmacea with special reference to the anatomy of *Pholadomya*".

MALACOLOGY COURSE IN KOREA. – On June 15-21, 1979, the Second Course on Malacology was presented at Yonsei University, Seoul, Republic of Korea, to interested university faculty, graduate students and secondary school teachers, by Dr. J.B. Burch, The University of Michigan, Ann Arbor, Michigan, U.S.A., Dr. Tadashige Habe, National Science Museum, Tokyo, Japan, and Dr. John I. Bruce, Dr. John C. Mallett and Mr. P.-R. Chung of the University of Lowell, Lowell, Massachusetts, U.S.A. The course was sponsored by Yonsei University and supported by the World Health Organization. The course covered such topics as systematics, evolution, distribution, ecology, culture methods, cytogenetics and medical malacology. It followed the pattern of the First Course on Malacology given in June 1978 at Yonsei University by most of the same lecturers. A similar course, enlarged in scope, is tentatively projected to be given in Korea in June 1980.

MEETING OF THE INSTITUTE OF MALACOLOGY. – The annual meeting of the Institute of Malacology was held at the Academy of Natural Sciences, Philadelphia, on December 1, 1978, presided over by the President, J.B. Burch. Others attending were Melbourne R. Carriker, George M. Davis, Robert Robertson, Clyde F.E. Roper, W.D. Russell-Hunter and S.K. Wu. The main business discussed was the affairs of *Malacologia*, which is sponsored by the Institute of Malacology. The following new officers were elected: President, Clyde F.E. Roper; President-Elect, Christopher J. Bayne; Vice President, S.K. Wu.

Malacologists attending the 1978 annual meeting of the Institute of Malacology. Left to right: W.D. Russell-Hunter, J.B. Burch, S.K. Wu, George M. Davis, Clyde F.E. Roper, Robert Robertson and Melbourne R. Carriker.

THE AMERICAN MALACOLOGICAL UNION Annual Meetings for 1980 will be held in Louisville, Kentucky, 19-25 July. Two symposia are scheduled: Feeding Mechanisms in Mollusks and Functional Morphology in Cephalopods. The local coordinator will be Mr. Walter Sage and the host organization will be the Louisville Conchological Society. For further information contact Dr. Clyde F.E. Roper, Department of Invertebrate Zoology (Mollusks), National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

THE SECOND INTERNATIONAL CONGRESS OF SYSTEMATIC AND EVOLUTIONARY BIOLOGY (ICSEB-II) will be held at The University of British Columbia, Vancouver, Canada, 17-24 July 1980. The provisional list of symposia topics include: Arctic refugia and the evolution of Arctic biota, origins and evolution of the North Pacific marine biota, evolution of reproductive strategies, evolutionary epigenetics, evolution of community structure, green algae and land plant origins, macromolecular mechanisms in evolution, allozymes and evolution, coevolution and foraging strategy, evolution of colonizing species, rare species and the maintenance of gene pools, and paleobiology of the Pacific Rim. Additional symposia may be included. Sessions for contributed papers and for papers in specialized fields, taxonomic as well as methodological, will also be organized. Those interested in receiving an information circular should write to Dr. G.G.E. Scudder, Department of Zoology, The University of British Columbia, 2075 Wesbrook Mall, Vancouver, B.C. V6T 1W5, Canada.

MEETINGS OF THE SOCIETY FOR EXPERIMENTAL AND DESCRIPTIVE MALACOLOGY. – The 1979 annual business meeting of the Society for Experimental and Descriptive Malacology will be held on December 1, 1979, in Ann Arbor, Michigan, U.S.A. The 1980 annual meeting will be held in Ann Arbor on February 2, 1980.

THE SEVENTH INTERNATIONAL MALACOLOGICAL CONGRESS, sponsored by the Unitas Malacologica, will be held from August 31 to September 6, 1980, in France at Perpignan and Banyuls-sur Mer. Perpignan is 15 kilometers from sandy shores, 30 from rocky shores and the "Laboratoire Arago", the biological station of the Universities of Paris, and 20 kilometers from the Pyrenean Mountains. Many scientific excursions will be possible for those interested in marine, brackish water and land molluscs.

The official languages of the Congress are English, French and German. Papers on all topics relating to living and fossil mollusks are welcomed. Potential participants should contact the Secrétariat du 7ème Congrès International de Malacologie, Laboratoire de B. I. M. et Malacologie, 55 Rue de Buffon, F-75005 Paris, France.

MALACOLOGICAL REVIEW, P. O. Box 420, Whitmore Lake, Michigan 48189, U.S.A.

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Organ der Deutschen Malakozoologischen Gesellschaft

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"ARGAMON"

Israel Journal of Malacology

published by

THE ISRAEL MALACOLOGICAL SOCIETY

and the

MUNICIPAL MALACOLOGICAL MUSEUM, NAHARIYA

"ARGAMON" and "LEVANTINA" (a Malacological Newsletter) are distributed free to Members of the Israel Malacological Society.

Membership fees : IL 50.— Domestic ; $ 7.— Foreign, payable to the Honorary Treasurer of the Israel Malacological Society, Dr. P. S. Tsuriel, 35 Weizmann St., Nahariya 22 404, Israel.

Manuscripts submitted for publication in "ARGAMON" are to be addressed to the Honorary Editor : H. K. Mienis, Kibbutz Netzer Sereni, 70-395, Israel. Address all other correspondence to The Israel Malacological Society, c/o Kibbutz Netzer Sereni, 70-395, Israel.

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DE NEDERLANDSE MALACOLOGISCHE VERENIGING

REDACTIE: Dr. A.C. van Bruggen en Dr. E. Gittenberger.
Redactie-adres: Rijksmuseum van Natuurlijke Historie, Raamsteeg 2, Postbus 9517, 2300 RA, Leiden.
De redactie wordt bijgestaan door een redactieraad van prominente malacologen.
Omslagontwerp: Dr. S. van der Spoel.

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of China

Vol. 4

November 1977

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Published by the
Malacological Society of China
No.2 Siang Yang Rd., Taipei
Taiwan Museum
Taiwan, R.O.C.

中華民國貝類學會刊行
發行人 劉棨
臺北市襄陽路2號 省立博物館
電話：3113261 3613963
中華民國・臺 灣

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GUIDA ILLUSTRATA ALL'IDENTIFICAZIONE
DELLE CONCHIGLIE DEL MEDITERRANEO

Bruno Sabelli e Gianni Spada

(dell'Istituto di Zoologia dell'Università di Bologna)

Fam. **Calyptraeidae** (fine) Gen. *Crepidula*

Fam. **Xenophoridae** Gen. *Xenophora*

Fam. **Aporrhaidae** Gen. *Aporrhais*

Supplemento a «Conchiglie» XIII (9-10), 1977

G.I. 05

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Fam. **Nassariidae I** Gen. *Nassarius*
Gen. *Naytiopsis*
Gen. *Amyclina*
Gen. *Arcularia*

Supplemento a «Conchiglie» XIII (9-10), 1977

Conchiglie

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DELLE CONCHIGLIE DEL MEDITERRANEO

Bruno Sabelli e Gianni Spada
(dell'Istituto di Zoologia dell'Università di Bologna)

Fam. **Nassariidae II** Gen. *Cyclope*
Gen. *Hinia*

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G.I. 07

GUIDA ILLUSTRATA ALL'IDENTIFICAZIONE
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Bruno Sabelli e Gianni Spada
(dell'Istituto di Zoologia dell'Università di Bologna)

Fam. **Naticidae II**
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Gen. *Bulbus*
Subfam. **Sininae** Gen. *Sinum*
Subfam. **Naticinae** Gen. *Natica*

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G.I. 08

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GUIDA ILLUSTRATA ALL'IDENTIFICAZIONE
DELLE CONCHIGLIE DEL MEDITERRANEO

Bruno Sabelli e Gianni Spada
(dell'Istituto di Zoologia dell'Università di Bologna)

Fam. **Mathildidae** Gen. *Mathilda*
Fam. **Turritellidae**
Subfam. **Turritellinae** Gen. *Turritella*
Subfam. **Pareorinae** Gen. *Mesalia*

Supplemento a «Conchiglie» XIV (3-6), 1978
G.I. 10

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Bruno Sabelli e Gianni Spada
(dell'Istituto di Zoologia dell'Università di Bologna)

Fam. **Lamellariidae** Gen. *Velutina*
Gen. *Lamellaria*

Fam. **Eratoidae** Gen. *Erato*
Gen. *Pusula*
Gen. *Trivia*

Supplemento a «Conchiglie» XIV (3-6), 1978
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HALIOTIS

1976
Vol. 7

ECOPHYSIOLOGIE DES MOLLUSQUES MARINS ET D'EAUX SAUMATRES

IMPACT DES POLLUTIONS

Observatoire de la mer (Fondation scientifique Ricard)

Ile des Embiez - Var - Septembre 1976

Publié par la Société Française de malacologie

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OF GREAT BRITAIN AND IRELAND

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THE PROSOBRANCH MOLLUSCS OF BRITAIN AND DENMARK

PART 2 — TROCHACEA

VERA FRETTER and ALASTAIR GRAHAM
Department of Zoology, University of Reading

The Prosobranch Molluscs of Britian and Denmark will be published as a series of supplements to *The Journal of Molluscan Studies*. They will appear irregularly as each part is ready. Part 4 — Rissoacea will appear with *The Journal of Molluscan Studies* vol. 44 pt. 3, December 1978. Parts may be purchased separately on application to the Editor or Publisher of the *Journal*.

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AN ANNOTATED CHECKLIST OF THE WESTERN ATLANTIC WARM WATER OPISTHOBRANCHS

EVELINE du BOIS-REYMOND MARCUS
C.P. 6994, 01000 São Paulo, Brazil.

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by

VERA FRETTER and ALASTAIR GRAHAM

Department of Zoology, University of Reading

Volume 44 — Part 2 — August 1978

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Printed in England by Entroform Limited, Reading.

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International Journal of Malacology
Revista Internacional de Malacologia
Journal International de Malacologie
Международный Журнал Малакологии
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Schnecken im waldigen Westteil der sogenannten „Weißen Mark" nördlich von Zwenkau bei Leipzig

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Taxonomic Revisions of the Living and Tertiary Marine Mollusca of the World

EDITED BY

R. TUCKER ABBOTT

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PART 1:
THE GENERA *RHINOCLAVIS, PSEUDOVERTAGUS* AND *CLAVOCERITHIUM*

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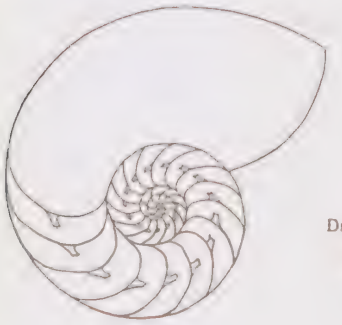

THE

NAUTILUS

EDITOR-IN-CHIEF
Dr. R. Tucker Abbott
American Malacologists, Inc.
Box 4208, Greenville, Delaware 19807

Mrs. Horace B. Baker
Business and Subscription Manager
11 Chelten Road
Havertown, Pennsylvania 19083

OFFICE OF PUBLICATION
American Malacologists, Inc.
429 B Arthur Drive, Hockessin, Delaware
Mail: Box 4208, Greenville, Delaware 19807

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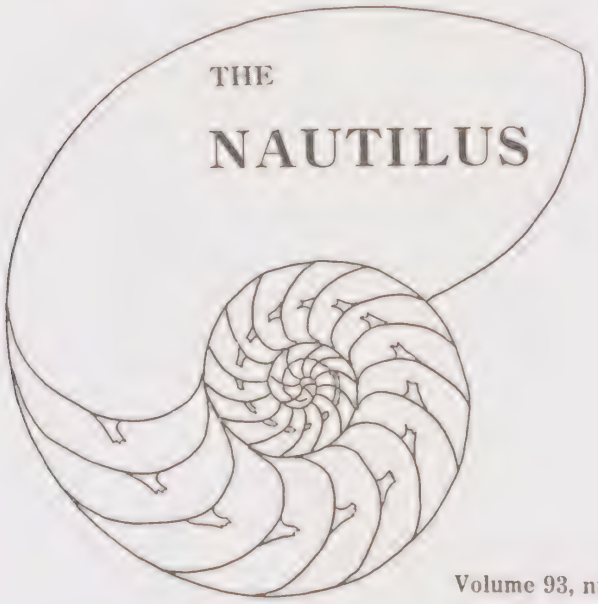

A quarterly devoted to malacology and the interests of conchologists

Founded 1889 by Henry A. Pilsbry.
Continued by H. Burrington Baker.
Editor-in-Chief: R. Tucker Abbott

THE
NAUTILUS
Volume 93, numbers 2–3 — April 23, 1979
ISSN 0028-1344

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CALIFORNIA MALACOZOOLOGICAL SOCIETY, INC.
Berkeley, California

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Distributed free to Members of the California Malacozoological Society, Inc.
Subscriptions (by Volume only) payable in advance to Calif. Malacozool. Soc., Inc.

Volume 21: $30.- plus postage ($1.- in U. S. A.; $2.50 to P. U. A. S.; $3.50 to all other foreign Countries, including Canada).
Single copies this issue $16.-. Postage extra.

Send subscription orders to California Malacozoological Society, Inc.
1584 Milvia Street, Berkeley, CA 94709, U. S. A.
Address all other correspondence to Dr. R. STOHLER, *Editor*, Department of Zoology
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VELIGER

A Quarterly published by
CALIFORNIA MALACOZOOLOGICAL SOCIETY, INC.
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Berkeley, California

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1584 Milvia Street, Berkeley, CA 94709, U. S. A.
Address all other correspondence to Dr. R. STOHLER, *Editor*, Department of Zoology
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ISSN 0042-3211

THE VELIGER

A Quarterly published by
CALIFORNIA MALACOZOOLOGICAL SOCIETY, INC.
Berkeley, California

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第36巻 第3号
Vol. 36, No. 3

日本貝類学会
Published by
THE
MALACOLOGICAL
SOCIETY OF JAPAN

昭和52年12月
December 1977

東京 Tokyo

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日本貝類学会

Published by
THE MALACOLOGICAL SOCIETY OF JAPAN

貝類学雑誌

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Published by
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CARLTON, James T., Department of Geology, University of California, Davis, California 95616, U.S.A. 140, 147
CARR, Robert Scott, Department of Biology, Texas A & M University, College Station, Texas 77843, U.S.A. 139
CARRIKER, Melbourne R., College of Marine Studies, Field Station, University of Delaware, Lewes, Delaware 19958, U.S.A. 124, 134, 141
CARROZZA, Ferdinando, c/o Banca Ameritalia, Via Arcivescovado 7, 10121 Torino, Italy 112
CASTAGNOLO, Lucio, Istituto di Anatomia Comparata, Laboratorio di Idrobiologia, Università degli Studi, Via delle Cerchia, 3, 53100 Siena, Italy 123
CATE, Crawford N., Invertebrate Zoology, Los Angeles County Museum of Natural History, 900 Exposition Blvd., Los Angeles, California 90007, U.S.A. 133
CERNOHORSKY, Walter O., Auckland Institute and Museum, Private Bag, Auckland, C. 1, New Zealand 132
CESARI, Paolo, Società Veneziana di Scienze Naturali, c/o Museo Civico di Storia Naturale, S. Croce 1730, 30125 Venezia, Italia 114

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CHERNOGORENKO, M.I., Hydrobiological Institute, Academy of Science, Ukrainian SSR, Kiev, U.S.S.R. 126
CHEVALLIER, Henry, Fustérouau, 32400 Riscle, France 116
CHIMENZ, Carla, Istituto di Zoologia, Università di Roma, Roma, Italia 123
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CHRISTENSEN, Carl C., 1612 Kamole Street, Honolulu, Hawaii 96821, U.S.A. 147
CHUKHCHIN, V.D., The Institute of Biology of Southern Seas, Academy of Science, Sevastopol, U.S.S.R. 126
CLARKE, Arthur H., National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, U.S.A. 109, 132
CLARKE, Bryan, Department of Genetics, University Park, Nottingham NG7 2RD, England 124
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CLENCH, William J., Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138, U.S.A. 109, 134
CLERGIER, M.P., Laboratoire de Biologie, Biochimie marines et Phycoécologie, Université de Poitiers, IUT de La Rochelle, 17026 La Rochelle, France 116
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CLOVER, Phillip W., P.O. Box 83, Glen Ellen, California 95442, U.S.A. 147
COAN, Eugene V., Department of Geology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118, U.S.A. 141, 147
COLLIN, Françoise, Laboratoire de Zoologie et Laboratoire maritime de Luc-sur-Mer, U.E.R. des Sciences de la Vie, Université de Caen, 14032 Caen, France 115
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COOPER, John W., Moss Landing Marine Laboratories, Moss Landing, California 95039, U.S.A. 147
CORPUZ, Gloria, Department of Biochemistry, College of Medicine, University of the Philippines, P.O. Box 593, Manila, Philippines 133
CORSELLI, Cesare, Via Postporta, 4, Gallarate, Italy 114
COSEL, Rudo von, I. Zoologisches Institut der Justus-Liebig-Universität, D-6300 Giessen, Germany (FR) 106
COWIE, R.H., Department of Zoology, Liverpool University, Liverpool L69 3BX, England 118
COX, John, Faculty of Natural Sciences, University of Tulsa, Tulsa, Oklahoma 74104, U.S.A. 147
CROTHERS, J.H., The Leonard Wills Field Centre, Nettlecombe Court, Williton, Taunton, Somerset TA4 4HT, England 120
CROWLEY, T.E., The Cottage, Church Street, Bampton, Oxford OX8 2NA, England 118
CRUZ, Lourdes J., Department of Biochemistry, College of Medicine, University of the Philippines, P.O. Box 593, Manila, Philippines 133
CVANCARA, A.M., Department of Geology, University of North Dakota, Grand Forks, North Dakota 58202, U.S.A. 131
DAGUZAN, Jacques, Laboratoire de Zoologie Générale et d'Ecophysiologie, Faculté des Sciences Biologiques, Université de Rennes, Avenue du Général Leclerc, 35042 Rennes Cedex, France 115, 116
DAPSON, Richard W., Biology Department, University of Michigan, Flint, Michigan 48503, U.S.A. 133
DAS, C.C., P.G. Department of Zoology, Berhampur University, Berhampur-7, Orissa, India 137

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FAVERIS, Roger, Laboratoire maritime de Luc-sur-Mer, Université de Caen, Esplanade de la Paix, 14032 Caen Cedex, France 115
FEDERICO, A. [complete address not given] 123
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FERAL, Colette, Laboratoire d'Endocrinologie et d'Embryologie expérimentales, U.E.R. des Sciences de la Vie, Equipe de Recherche associée au C.N.R.S., no. 491, 14032 Caen Cedex, France 115
FERENC, Magda, Egyetem u. 2-6, 6722 Szeged, Hungary 135
FERREIRA, Antonio J., 2060 Clarmar Way, San Jose, California 95128, U.S.A. 138, 141
FIGUERAS, Alfredo LAGUARDA-, Universidad Nacional Autónoma de México, Centro de Ciencias del Mar y Limnologia, México 20, D.F., Mexico 145
FINLAY, C. John, 116 Tanglewood Lane, Newark, Delaware 19711, U.S.A. 133
FISCHER, P.-H., 18/55 Prince Albert Street, Mosman, N.S.W. 2088, Australia 117
FISH, J.D., Department of Zoology, University College of Wales, Aberystwyth, Wales 121
FLASAR, Ivo, Oblastní vlastivědné museum, Zámecké náměsti 14, 415 01 Teplice v Čechách, ČSSR 128
FORCART, Lothar, Naturhistorisches Museum, Basel, Switzerland 118
FOSTER-SMITH, R.L., Dove Marine Laboratory, Cullercoats, North Shields, Tyne and Wear, Northumberland, U.K. 121
FRANCHINI, Dario, Via Cremona 37, 46100 Mantova, Italy 114
FRANK, Christina, Prankergasse 71, A-8020 Graz, Austria 135
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FREEMAN, P.G., 314 Belmont Road, Grand Forks, North Dakota 58201, U.S.A. 131
FRENCH, John Robert Putnam, III, Museum of Zoology, The University of Michigan, Ann Arbor, Michigan 48109, U.S.A. 110
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FREST, Terrence J., The University of Iowa, Iowa City, Iowa 52242, U.S.A. 141
FRETTER, Vera, Department of Zoology, University of Reading, Whiteknights, Reading RG6 2AJ, England 120, 121
FTOMOV, A.S., Hydrobiological Institute, Academy of Science, Ukrainian SSR, Kiev, U.S.S.R. 125
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FULLINGTON, Kate E., Department of Biology, North Texas State University, Denton, Texas 76201, U.S.A. 131
FULLINGTON, Richard W., Dallas Museum of Natural History, P.O. Box 26193, Fair Park Station, Dallas, Texas 75226, U.S.A. 131, 132, 136
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GAIDASH, Yu. K., Dnepropetrovsk State University, Dnepropetrovsk, U.S.S.R. 125
GALAGAN, N.P., Hydrobiological Institute, Academy of Science, Ukrainian SSR, Kiev, U.S.S.R. 126
GALASSI, Silvana, Istituto di Biologia del Mare, CNR, Riva Sette Martiri 1363/A, 30122 Venezia, Italia 123
GALPERINA, G.E., All-Union Research Institute of Fishery and Oceanography, Moscow, U.S.S.R. 126
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GERARD, André, Laboratoire de Zoologie, Aquaculture et Pollution Marines, Faculté des Sciences, 6 Avenue Le Gorgeu, 29283 Brest Cedex, France 116
GETZ, Lowell L., Department of Ecology, Ethology and Evolution, University of Illinois, Urbana, Illinois 61801, U.S.A. 133
GHISOTTI, Fernando, Via Giotto 9, 20145 Milano, Italy 112, 113, 114
GHOSE, K.C., Department of Zoology, University of Calcutta, 35 B.C. Road, Calcutta 700019, India 141

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GIBSON, M.A., Department of Biology, Acadia University, Wolfville, Nova Scotia B0P 1X0, Canada 141
GILBERT, Mary Ann, 1017 South Main Street, Ottawa, Kansas 66067, U.S.A. 131
GILBERTSON, Donald, Department of Ecology and Behavioral Biology, University of Minnesota, Minneapolis, Minnesota 55455, U.S.A. 122
GILMAN, E.V., Hydrobiological Institute, Academy of Science, Ukrainian SSR, Kiev, U.S.S.R. 125
GIORDANI SOIKA, Antonio, Museo Civico di Storia Naturale di Venezia, 30125 Venezia, Italia 123
GIROD, Alberto, Acquario Civico, Stazione Idrobiologica, Milano, Italy 123
GITTENBERGER, E., Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands 108
GIUSTI, Folco, Istituto di Zoologia dell'Università, Via Mattioli 4, 53100 Siena, Italia 123
GLADENKOV, Yuri B., Geological Institute, Academy of Sciences, Moscow 109017, U.S.S.R. 127, 139
GLÉMAREC, M., Laboratoire d'Océanographie Biologique, Institut d'Etudes Marines, Faculté des Sciences, 29283 Brest Cedex, France 116
GOLIKOV, Alexandre N., Zoological Institute, Academy of Sciences of the U.S.S.R., Leningrad B-164, U.S.S.R. 126
GONTYA, F.A., Pedagogical Institute, Tiraspol, U.S.S.R. 125
GOOCH, Charles, E & D Building, Tennessee Valley Authority, Muscle Shoals, Alabama 35660, U.S.A. 134
GOODWIN, B.J., Portway School, Penpole Lane, Shirehampton, Bristol, England 121, 122
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GOSLINER, Terrence M., Zoology Department, University of New Hampshire, Durham, New Hampshire 03824, U.S.A. 134
GÖTTING, Klaus-Jürgen, Zoologisches Institut der Justus Liebig-Universität, Stephanstr. 24, D-63 Giessen, Germany (FR) 106
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GRAHAM, Alastair, Department of Zoology, University of Reading, Whiteknights, Reading RG6 2AJ, England 120, 121
GRAVES, Debra A., Department of Biology, Acadia University, Wolfville, Nova Scotia B0P 1X0, Canada 141
GRECCHI, Glauco, Via Cenisio 74, 20154 Milano, Italy 114
GRIGORIEV, B.F., Hydrobiological Institute, Academy of Science, Ukrainian SSR, Kiev, U.S.S.R. 125
GUGLER, Carl W., School of Life Sciences, University of Nebraska, Lincoln, Nebraska 68588, U.S.A. 109
GUILLOU, Jacques, Laboratoire d'Océanographie Biologique, Faculté des Sciences et Techniques, Université de Bretagne Occidentale, 29283 Brest Cedex, France 116
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GUPTA, G.P., Indian Agricultural Research Institute, Port Blair, South Andaman, India 138
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HAMOUI, Adel, Département de Zoologie, Faculté des Sciences, Université de Damas, Damas, République Arabe Syrienne 115
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HARRIS, Larry G., Department of Zoology, University of New Hampshire, Durham, New Hampshire 03824, U.S.A. 138
HARTWICK, B., Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia V5A 1S6, Canada 139
HATFIELD, Edward B., Jackson Estuarine Laboratory, University of New Hampshire, R.F.D. No. 1, Adams Point, Durham, New Hampshire 03824, U.S.A. 133
HAVEN, Dexter S., Virginia Institute of Marine Science, Gloucester Point, Virginia 23062, U.S.A. 137
HEARD, William H., Department of Biological Science, Florida State University, Tallahassee, Florida 32306, U.S.A. 109
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HERLIN, P., Laboratoire de Zoologie et Laboratoire maritime de Luc-sur-Mer, U.E.R. des Sciences de la Vie, Université de Caen, 14032 Caen, France 115
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HOMAN, William C., Department of Biology, Bucknell University, Lewisburg, Pennsylvania 17837, U.S.A. 139
HOMMAY, Gérard, Laboratoire de Zoologie Générale et d'Ecophysiologie, Faculté des Sciences Biologiques, Université de Rennes, 35042 Rennes Cedex, France 116
HORNBACH, Daniel J., Department of Zoology, Miami University, Oxford, Ohio 45056, U.S.A. 109
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HOUBRICK, Richard S., Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, U.S.A. 130, 131
HOUSTON, Roy S., Department of Biology, Loyola Marymount University, Los Angeles, California 90045, U.S.A. 137
HUBENDICK, Bengt, Naturhistoriska Museet, Göteborg, 40030, Sweden 107
HUGHES, Roger N., Department of Zoology, University College of North Wales, Bangor, Gwynedd LL57 2UW, U.K. 141
HUGHES, T.G., Suakin Marine Laboratory, P.O. Box 24, Port Sudan, Sudan 120
HULET, William H., The Marine Biomedical Institute, University of Texas Medical Branch, Galveston, Texas 77550, U.S.A. 141
HYLLEBERG, J., Department of Ecology and Genetics, Ny Munkegade, University of Arhus, 8000 Arhus C, Denmark 120
IBÁÑEZ, M., Department of Zoology, Science Faculty, University of Granada, Granada, Spain 106, 118
IBARAKI, Masako, Geoscience Institute, Faculty of Science, Shizuoka University, Shizuoka 422, Japan 139

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ILJINA, L.B., Palaeontological Institute, Academy of Sciences, Moscow, U.S.S.R. 127
INABA, Akihiko, Mukaishima Marine Biological Station of Hiroshima University, Mukaishima-cho, Onomichi P.O., Hiroshima-ken, Japan 146
ISOM, Billy G., Environmental Biology Branch, Division of Environmental Research and Development, Tennessee Valley Authority, Muscle Shoals, Alabama 35660, U.S.A. 134
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IVANEGA, I.G., Hydrobiological Institute, Academy of Science, Ukrainian SSR, Kiev, U.S.S.R. 125
IVANKOVA, A.F., Moscow State University, Moscow, U.S.S.R. 125
IZZATULLAJEV, Z.I., Institute of Zoology and Parasitology, Academy of Sciences of Tadzhik SSR, Dushanbe, U.S.S.R. 125
JABAROV, D.G., Institute of Zoology, Academy of Science, Azerbaijan SSR, Baku, U.S.S.R. 125
JACOBSON, Morris K., 865 Capone Street, S.E., Palm Bay, Florida 32905, U.S.A. 131, 137, 141
JAMES, Matthew J., Moss Landing Marine Laboratories, P.O. Box 223, Moss Landing, California 95039, U.S.A. 147
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JANSSEN, Ronald, Forschungs-Institute Senckenberg, Senckenberganlage 25, 6000 Frankfurt am Main 1, Federal Republic of Germany 106
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JELNES, Jens Erik, Danish Bilharziasis Laboratory, Jaegersborg Alle 1 D, DK-2920 Charlottenlund, Denmark 106
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JOKINEN, Eileen H., Biology Department, Suffolk University, Boston, Massachusetts 02114, U.S.A. 133
JONES, Douglas S., Department of Geological and Geophysical Sciences, Princeton University, Princeton, New Jersey 08540, U.S.A. 133
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KAFANOV, Alexander I., Zoological Institute, Academy of Sciences of the U.S.S.R., Leningrad B-164, U.S.S.R., and Institute of Biology of the Sea, Far Eastern Scientific Center, Academy of Sciences, Vladivostok, U.S.S.R. 126
KANEV, G.P., Institute of Geology, Komi-filial Academy of Sciences, Syktyvkar, U.S.S.R. 127
KANIE, Yasumitsu, Yokosuka City Museum, Yokosuka, Japan 146
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KEFERL, Eugene P., Division of Natural Science, Brunswick Junior College, Brunswick, Georgia 31520, U.S.A. 109
KELLOGG, Michael G., Moss Landing Marine Laboratories, Moss Landing, California 95039, U.S.A. 147
KENK, Vida C., Department of Biological Sciences, San Jose State University, San Jose, California 95192, U.S.A. 147

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D'ATTILIO, Anthony, Department of Invertebrate Zoology, San Diego Museum of Natural History, Balboa Park, P.O. Box 1390, San Diego, California 92112, U.S.A. 106, 121, 133, 137
DAVIS, George M., Department of Malacology, Academy of Natural Sciences, 19th and the Parkway, Philadelphia, Pennsylvania 19103, U.S.A. 109, 124
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DAY, Robert Marshall, Department of Biology, University of California, Irvine, California 92717, U.S.A. 138
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DENNIS, Sally D., Forestry, Fisheries, and Wildlife Development, Tennessee Valley Authority, Norris, Tennessee 37828, U.S.A. 134, 136
DEWARUMEZ, Jean-Marie, Institut de Biologie maritime et régionale, Avenue Foch, 62930 Wimereux, France 115
DILLON, Robert T., Jr., Department of Biology, The University of Pennsylvania, Philadelphia, Pennsylvania 19103, U.S.A. 109
DMITRIEVA, E.F., Leningrad Agricultural Institute, Leningrad, U.S.S.R. 125
DOGUZHAYEVA, L.A., Zoological Institute, Academy of Sciences of the U.S.S.R., Leningrad B-164, U.S.S.R. 127
DOLGIN, V.N., Tomsk Pedagogical Institute, Tomsk State University, Tomsk, U.S.S.R. 125
DOMOKOS, Tamás, Szarvasi u. 71, 5600 Békéscsaba, Hungary 135
DONAT, Winfield, III, Naval Postgraduate School, Monterey, California 93940, U.S.A. 138
DRAPER, Bertram C., Malacology Section, Los Angeles County Museum of Natural History, 900 Exposition Blvd., Los Angeles, California 90007, U.S.A. 147
DROZDOWSKI, Arnold, Instytut Biologii, Uniwersytetu M. Kopernika w Toruniu, ul. Gagarina 11, 87-100 Toruń, Poland 128
DRUSHCHITS, V.V., Zoological Institute, Academy of Sciences of the U.S.S.R., Leningrad B-164, U.S.S.R. 127
DUFRENNE, M., Laboratoire de Biologie et Biochimie Marines, U.E.R. Sciences Fondamentales et Appliquées, Université de Poitiers, Institut Universitaire de Technologie de La Rochelle, 17026 La Rochelle Cedex, France 115
DUNDEE, Dee S., Department of Biological Science, University of New Orleans, New Orleans, Louisiana 70122, U.S.A. 109, 131
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DuSHANE, Helen, 15012 El Soneto Drive, Whittier, California 90605, U.S.A. 140
DUSSART, G.B.J., North West Water Authority, Rivers Division, Chertsey Hill, London Road, Carlisle CA1 2QX, England 121
DVORYADKIN, V.A., Biological-Pedological Institute, Academy of Sciences, Vladivostok, U.S.S.R. 127
DYGA, A.K., Dnepropetrovsk State University, Dnepropetrovsk, U.S.S.R. 126
EDMUNDS, Malcolm, Biology Division, Preston Polytechnic, Corporation Street, Preston PR1 2TQ, U.K. 120, 121
EDWARDS, Nicholas, 52 Little Paddocks, Ferring, Worthing, Sussex BN12 5NH, England 118
EGOROVA, E.N., Zoological Institute, Academy of Sciences of the U.S.S.R., Leningrad B-164, U.S.S.R. 126
ELLIS, C.J., Department of Zoology, Liverpool University, Liverpool L69 3BX, England 118
ELOUARD, Pierre, Département des Sciences de la Terre, Université Claude-Bernard – Lyon I, 43, Bd du 11 Novembre 1918, 69621 Villeurbanne, France 123
EMERSON, William K., Department of Living Invertebrates, American Museum of Natural History, Central Park West at 79th, New York, New York 10024, U.S.A. 132, 133
EMERY, K.O., Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543, U.S.A. 132
ESCOUBET, Pierre, Fondation Scientifique Ricard, Observatoire de la Mer, Ile des Embiez, Le Brusc, 83140 Six-Fours-les-Plages, France 115
EVERSOLE, Arnold G., Department of Entomology and Economic Zoology, Clemson University, Clemson, South Carolina 29631, U.S.A. 109, 122
FANKBONER, P.V., Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia V5A 1S6, Canada 139
FARMER, Wesley M., 1327 East Donner Drive, Tempe, Arizona 85282, U.S.A. 137
FASULO, Giuseppe, Via Luca Giordano, 82, Napoli, Italy 113
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KESSLER, John, R.R. 4, Taylorsville, Kentucky 40071, U.S.A. 132
KILMER, Frank H., Department of Geology, Humboldt State University, Arcata, California 95521, U.S.A. 139
KIM, Ny, Laboratoire maritime de Luc-sur-Mer, Université de Caen, 14032 Caen Cedex, France 115
KIPP, Ronald, Biology Department, College of Staten Island, Staten Island, New York 10301, U.S.A. 109
KIRILLOV, V.A., Pedagogical Institute, Blagoveshchensk, U.S.S.R. 126
KISS, János Botond, Str. 23 August, Bloc H1, Sc. A, Ap. 3, Tulcea, Romania 135
KITIZINA, L.A., Hydrobiological Institute, Academy of Science, Ukrainian SSR, Kiev, U.S.S.R. 126
KLAPPENBACH, Miguel A., Museo Nacional de Historia Natural, Montevideo, Uruguay 111
KLINGER, H.C., South African Museum, P.O. Box 61, Cape Town, 8000, South Africa 121
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KOHL, Roy F., Department of Geology, Humboldt State University, Arcata, California 95521, U.S.A. 141
KOKAI, Frank L., Museum of Zoology, The Ohio State University, Columbus, Ohio 43210, U.S.A. 109
KONDRATENKOV, A.P., Zoological Institute, Academy of Sciences of the U.S.S.R., Leningrad B-164, U.S.S.R. 126
KORRINGA, P., Institut Néerlandais pour les recherches concernant la Pêche, Ijmuiden, Pays-Bas 115
KOSENKO, L.A., Institute of Biology of the Sea, Academy of Sciences, Vladivostok, U.S.S.R. 126
KOTAKA, Tamio, Institute of Geology and Paleontology, Faculty of Science, Tohoku University, Sendai, Japan 139
KOVÁCS, Gyula, Deák u. 3, 5600 Békéscsaba, Hungary 135
KRAEMER, Louise Russert, Department of Zoology, University of Arkansas, Fayetteville, Arkansas 72701, U.S.A. 109
KRAKATITZA, T.F., Azov and Black Sea Research Institute of Fishery and Oceanography, Kerch, U.S.S.R. 126
KRASNOV, E.V., Institute of Biology of the Sea, Academy of Sciences, Vladivostok, U.S.S.R. 127
KRESTIANINOV, Ju. S., Ural Scientific Institute of Water-economy, Chelabinsk, U.S.S.R. 125
KRISALNY, V.A., Hydrobiological Institute, Academy of Science, Ukrainian SSR, Kiev, U.S.S.R. 126
KROLOPP, Endre, Magyar Állami Földtani Intézet, Népstadion u. 14, 1143 Budapest, Hungary 135
KRUGLOV, N.D., Pedagogical Institute, Smolensk, U.S.S.R. 126
KUBODERA, Tsunemi, Faculty of Fisheries, Hokkaido University, Hakodate, Hokkaido, Japan 142
KUIPER, J.G.J., Institut Neerlandais, 121 Rue de Lille, Paris 7e, France 123
KULAKOVSKY, E.E., Zoological Institute, Academy of Sciences of the U.S.S.R., Leningrad B-164, U.S.S.R. 126
KURODA, Tokubei, 41, Tanaka, Minami-Okubo-cho, Sakyo, Kyoto, Japan 145
KUSHLAN, James A., U.S. National Park Service, Everglades National Park, Homestead, Florida 33030, U.S.A. 131
KUZIRIAN, Alan M., Department of Zoology, University of New Hampshire, Durham, New Hampshire 03824, U.S.A. 121
LaFOLLETTE, Patrick I., Malacology Section, Los Angeles County Museum of Natural History, 900 Exposition Blvd., Los Angeles, California 90007, U.S.A. 147
LAI, K.Y., The Taiwan Museum, Taipei, Taiwan, Republic of China 110
LAN, Tsu-Chiao, 40, Lane 105, Liao-ning Street, Taipei, Taiwan, Republic of China 110
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LAZARIDOU-DIMITRIADOU, Maria, Laboratoire de Zoologie, Université de Thessalonique, Thessalonique, Grece 116
LE BORGNE, Yves, Société Atlantique de Mariculture, 50760 Barfleur, France 116
LEE, Richard M., Bigelow Laboratory for Ocean Sciences, West Boothbay Harbor, Maine 04575, U.S.A. 132
LEEDOM, Walter S., Department of Biological Science, Florida State University, Tallahassee, Florida 32306, U.S.A. 132
LE GALL, Jean-Yves, Centre Océanologique de Bretagne/CNEXO, 29273 Brest Cedex, France 116
LE GALL, Pierre, Laboratoire Maritime, 14530 Luc-sur-Mer, France 116
LELONG, Patrick, Fondation Scientifique Ricard, Observatoire de la Mer, île des Embiez, Le Brusc, 83140 Six-Fours-les-Plages, France 115
LE MOAL, Yveline, Laboratoire d'Océanographie Biologique, Faculté des Sciences et Techniques, Université de Bretagne Occidentale, 29283 Brest Cedex, France 116
LE ROUX, Sylvie, Laboratoire de Zoologie, Aquaculture et Pollutions Marines, Faculté des Sciences, Université de Bretagne Occidentale, 29279 Brest Cedex, France 115
LESHKO, Ju. V., Komi Department of the All-Union Hydrobiological Society, Siktivkar, U.S.S.R. 125
LEVINA, O.V., Hydrobiological Institute, Academy of Science, Ukrainian SSR, Kiev, U.S.S.R. 126
LIKHAREV, I.M., Zoological Institute, Academy of Sciences of the U.S.S.R., Leningrad B-164, U.S.S.R. 125
LINDBERG, David R., Center for Coastal Marine Studies, University of California, Santa Cruz, California 95064, U.S.A. 134, 137, 147
LINSLEY, Robert M., Department of Geology, Colgate University, Hamilton, New York 13346, U.S.A. 124
LITTLE, Colin, Department of Zoology, Bristol University, Bristol BS8 1UG, England 121
LOGVINENKO, B.M., Moscow State University, Moscow, U.S.S.R. 126
LUBET, Pierre, Laboratoire de Zoologie, U.E.R. des Sciences de la Vie, Université de Caen, 14032 Caen Cedex, France 115
LUBJANOV, I.P., Dnepropetrovsk State University, Dnepropetrovsk, U.S.S.R. 125
LUCAS, Albert, Laboratoire de Zoologie, Aquaculture et Pollutions Marines, Faculté des Sciences, Université de Bretagne Occidentale, 29283 Brest Cedex, France 116
LUEGER, Josef P., Karolinengasse 7/13b, A-1040 Wien, Austria 106
LUKASHEVA, T.A., Southern Department of the Institute of Oceanology, Academy of Sciences, Gelendzik, U.S.S.R. 126
LUTZ, Richard A., Department of Geology and Geophysics, Yale University, New Haven, Connecticut 06520, U.S.A. 109
LYONS, William G., Florida Department of Natural Resources, Marine Research Laboratory, St. Petersburg, Florida 33701, U.S.A. 132
MAASSEN, W.J.M. [no address given] 108
MACE, Anne-Marie, Station Marine d'Endoume, rue Batterie des Lions, 13007 Marseille, France 116
MacINTOSH, Richard A., Northwest and Alaska Fisheries Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 2725 Montlake Blvd. East, Seattle, Washington 98112, U.S.A. 141
MACKIE, G.L., Department of Zoology, University of Guelph, Guelph, Ontario N1G 2W1, Canada 109, 131, 133
MAGALDI, Norman H., Museo Argentino de Ciencias Naturales, "Bernardino Rivadavia", Buenos Aires, Argentina 111
MAKHONINA, A.V., Dnepropetrovsk State University, Dnepropetrovsk, U.S.S.R. 126
MAKOGON, Kh. G., Zooveterinary Institute, Lvov, U.S.S.R. 126
MALAREVSKAJA, A. Ya., Hydrobiological Institute, Academy of Science, Ukrainian SSR, Kiev, U.S.S.R. 126
MALEK, Emile A., Department of Tropical Medicine, Tulane University Medical Center, New Orleans, Louisiana 70112, U.S.A. 131

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MALEK, Rebecca R., Department of Tropical Medicine, Tulane University Medical Center, New Orleans, Louisiana 70112, U.S.A. 131
MANE, U.H., Department of Zoology, Marathwada University, Aurangabad, Maharashtra, India 122
MANLY, Ralph, School of Chemical and Physical Sciences, Kingston Polytechnic, Penrhyn Road, Kingston upon Thames KT1 2EE, Surrey, England 121
MAPES, Royal H., Ohio University, Athens, Ohio 45701, U.S.A. 138, 141
MAPSTONE, Gillian M., Department of Zoology, La Trobe University, Bundoora 3083, Victoria, Australia 119
MARASTI, Raffaella, Istituto di Geologia e Paleontologia, Università di Parma, Parma, Italy 123
MARCUS, Eveline du Bois-Reymond, Caixa Postal 6994, 01000 São Paulo, S.P., Brazil 120
MARELLI, Dan C., Department of Biological Sciences, San Francisco State University, San Francisco, California 94132, U.S.A. 138, 147
MARIANI, Mauro, Biology Group, Ispra, D.G. Research, Science and Education, C.E.C. Euratom J.R.C., 21020 Ispra, Italy 123
MARTIN, Yvan, Fondation Scientifique Ricard, Observatoire de la Mer, île des Embiez, Le Brusc, 83140 Six-Fours-les-Plages, Var, France 115
MARTINEZ, Jean-Claude, Laboratoire de Zoologie, Aquaculture et Pollutions Marines, Faculté des Sciences, 6 Avenue Le Gorgeu, 29283 Brest Cedex, France 116
MARTINSON, G.G., Institute of Limnology, Academy of Sciences, Leningrad, U.S.S.R. 127
MASAHITO, Prince [ref. T. Habe, National Science Museum, Ueno Park, Tokyo, Japan] 143
MASSÉ, Henri, Station maritime d'Endoume, 13007 Marseille, France 115
MASSON, Michel, Laboratoire de Radioécologie marine, C.E.A., B.P. 270, 50107 Cherbourg, France 115
MASUDA, Kôichirô, Department of Geology, Miyagi University of Education, Aoba, Sendai 980, Japan 139
MATEKIN, P.V., Moscow State University, Moscow, U.S.S.R. 125
MATHER, Jennifer A., Department of Psychology, Brandeis University, Waltham, Massachusetts 02154, U.S.A. 139
MATHIEU, Michel, Laboratoire de Zoologie et Laboratoire maritime de Luc-sur-Mer, U.E.R. des Sciences de la Vie, Université de Caen, 14032 Caen, France 115
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MATVEEVA, T.A., Zoological Institute, Academy of Sciences of the U.S.S.R., Leningrad B-164, U.S.S.R. 126
McCULLOUGH, Jack D., Department of Biology, Stephen F. Austin State University, Nacogdoches, Texas 75962, U.S.A. 133
McDONALD, Gary R., P.O. Box 535, Aromas, California 95004, U.S.A. 138
McLEOD, M.J., Department of Zoology and Academic Computer Service, Miami University, Oxford, Ohio 45056, U.S.A. 109
McMAHON, Robert F., Department of Biology, The University of Texas, Arlington, Texas 76019, U.S.A. 121
MEGURO, Kiyomi, Chiba Prefectural Fisheries Experiment Station, Chikura-machi, Awagun, Chiba Prefecture, Japan 142
MELIKOV, Yu. F., Institute of Zoology, Academy of Science, Azerbaijan SSR, Baku, U.S.S.R. 125
MELONE, Giulio Cesare, Via Celoria 10, 20133 Milano, Italy 123
MERÉNYI, László, Postafiók 76, 3101 Salgótarján, Hungary 135
MERRILL, Arthur S., Northeast Fisheries Center, Woods Hole, Massachusetts 02543, U.S.A. 131, 132
METCALF, Artie L., Department of Biological Sciences, University of Texas, El Paso, Texas 79968, U.S.A. 132
MEZZADRI, M.G., Istituto di Zoologia, Università di Parma, Parma, Italy 123
MIENIS, Henk K., Zoological Museum, Mollusc Collection, Hebrew University, Jerusalem, Israel 107
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MILLER, Andrew, 225 Creek Road, Sellersburg, Indiana 47172, U.S.A. 132
MILLER, Barry B., Department of Geology, Kent State University, Kent, Ohio 44242, U.S.A. 125

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MILLER, Mabel Fentress, Environmental Education Program, Science Education Department, Dade County Public Schools, 1410 Northeast Second Avenue, Miami, Florida 33132, U.S.A. 134
MINATO, Hiroshi, Kumano Senior High School, Kamitonda-Cho, Wakayama-Ken, 649-21, Japan 143, 144, 145
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MINICHEV, Yu. S., Leningrad State University, Leningrad, U.S.S.R. 125
MIRKES, P.E., Department of Biology, University of South Carolina, Columbia, South Carolina 29208, U.S.A. 134
MITCHELL-TAPPING, Hugh J., 6101 Warwick Court, New Orleans, Louisiana 70114, U.S.A. 134
MITRA, S.C., Zoological Survey of India, 8 Lindsay Street, Calcutta 700016, India 125
MIURA, Hiroko, Zoological Laboratory, Fukuoka Women's University, Kasumigaoka, Higashiku, Fukuoka 813, Japan 146
MONOD, Jean-Louis, Laboratoire d'Hydrobiologie, Faculté de Pharmacie, La Timone, 13008 Marseille, France 115
MOORE, Donald R., Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, Florida 33149, U.S.A. 109, 132, 134
MORDAN, P.B., Department of Zoology, British Museum (Natural History), Cromwell Road, London SW7, England 118
MORETEAU, Jean-Claude, Laboratoire de Zoologie bât. 442, Université Paris-Sud Centre d'Orsay, 91405 Orsay, France 115
MORRICONI, Elba Rosa, Instituto de Biologia Marina y Pesquera, San Antonio Oeste, Rio Negro, Argentina 116
MORRIS, John S., Department of Biological Sciences, Marshall University, Huntington, West Virginia 25701, U.S.A. 133
MORRISON, Joseph P.E., Division of Mollusks, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20506, U.S.A. 109
MORTON, Brian, Department of Zoology, The University of Hong Kong, Hong Kong 120, 122
MOSKALEV, L.I., Institute of Oceanology, Academy of Sciences, Moscow, U.S.S.R. 126
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MUNARI, Lorenzo, Museo Civico di Storia Naturale, Fontego dei Turchi, 30125 Venezia, Italia 123
MÜNZING, Klaus, Albertstrasse 5, D-7800 Freiburg i. Br., Germany (DR) 129
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MURTY, A.S., Department of Zoology, Hindu College, Machilipatnam, A.P., India 121
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NAKANO, Daisaburo, Toba Aquarium, Toba, Mie Prefecture 517, Japan 146
NARDI, Pietro Angelo, Via Lanfranco 6, 27100 Pavia, Italy 123
NECRASOVA, M. Ja., All-Union Research Institute of Fishery and Oceanography, Moscow, U.S.S.R. 126
NEGUS, P.E., 82 Chelsea Gardens, Chelsea Bridge Road, London SW1W 8RQ, England 118
NELSON, Clifford M., U.S. Geological Survey, Reston, Virginia 22092, U.S.A. 139
NESIS, K.N., Institute of Oceanology, Academy of Sciences, Moscow, U.S.S.R. 126, 127
NEVESSKAYA, L.A., Palaeontological Institute, Academy of Sciences, Moscow, U.S.S.R. 127
NICHOLS, Jean Ann, Marine Institute, University of Georgia, Sapelo Island, Georgia 31327, U.S.A. 133
NICOL, David, Department of Geology, University of Florida, Gainesville, Florida 32611, U.S.A. 132
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NODA, Hiroshi, Institute of Geoscience, University of Tsukuba, Japan 143
NORDSIECK, Hartmut, Johannesstrasse 38, D-722 Schwenningen, Germany (FR) 106
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NYBAKKEN, James W., Moss Landing Marine Laboratories, Box 223, Moss Landing, California 95039, U.S.A. 138
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ODIETE, W.O., Department of Biological Sciences, University of Lagos, Akoka, Lagos, Nigeria 122
OKUTANI, Takashi, Tokai Regional Fisheries Research Laboratory, Tokyo, Japan 138, 142, 144, 146
OLAZARRI, José, Museo Nacional de Historia Natural, Montevideo, Uruguay 111
OLD, William E., Jr., Department of Living and Fossil Invertebrates, The American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024, U.S.A. 109, 133, 147
OLIVERA, Baldomero M., Department of Biology, University of Utah, Salt Lake City, Utah 84112, U.S.A. 133
OXFORD, G.S., Department of Biology, University of York, Heslington, York YO1 5DD, England 124
OYAMA, Katura, Geological Survey, Tokyo, Japan 146
PACE, Gary L., Biology Department, University of Michigan, Flint, Michigan 48503, U.S.A. 133
PAIN, T., 47 Reynolds House, Millbank, London SW1P 4HP, England 118
PANETTA, Pietro, Istituto Sperimentale Talassografico, via Roma 3, 74100 Taranto, Italia 123
PANFILOV, B.G., Institute of Oceanology, Academy of Sciences, Moscow, U.S.S.R. 127
PARAMONOVA, N.P., Palaeontological Institute, Academy of Sciences, Moscow, U.S.S.R. 127
PARISI, V., Istituto di Zoologia, Università di Parma, Parma, Italy 123
PARIVAR, K., Department of Biology, School of Sciences, Ferdowsi University, Mashhad, Iran 122
PARKER, E. Davis, Jr., Department of Biology, University of Rochester, Rochester, New York 14627, U.S.A. 137
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PASCUAL, Emilio, Instituto de Investigaciones Pesqueras, Cadix, Espagne 115
PAUL, C.R.C., Department of Geology, Liverpool University, Liverpool L69 3BX, England 118
PECHENIK, Jan A., Graduate School of Oceanography, University of Rhode Island, Kingston, Rhode Island 02881, U.S.A. 139
PENATI, Clara, Istituto di Ecologia Animale ed Etologia, Università di Pavia, Pavia, Italy 123
PENCREACH, Danielle, Centre Océanologique de Bretagne, Equipe Pêche, B.P. 337, 29273 Brest Cedex, France 116
PERRON, Frank E., Department of Zoology, University of Hawaii, Honolulu, Hawaii 96822, U.S.A. 121, 124
PETIT, Henri, Laboratoire de Zoologie, Aquaculture et Pollutions Marines, Faculté des Sciences, 6 Avenue Le Gorgeu, 29283 Brest Cedex, France 116
PETIT, Richard E., P. O. Box 30, North Myrtle Beach, South Carolina 29582, U.S.A. 109
PETRAITIS, Peter S., Department of Ecology and Evolution, State University of New York, Stony Brook, New York 11794, U.S.A. 139
PEZZOLI, Enrico, Istituto di Zoologia, Via Mattioli 4, Siena, Italia 123
PIANI, Piero, Via delle Fragole, Cas. post. 2207, Bologna E.L. 23, 40137 Bologna, Italy 112, 114
PICTON, B.E., Ulster Museum, Belfast, Northern Ireland 118
PINTÉR, István, Móricz Zsigmond u. 1, 8360 Keszthely, Hungary 135
PINTÉR, László, Magyar Nemzeti Muzeum Állattár, Baross u. 13, H-1088 Budapest, Hungary 106, 135
PITA, Jorge, Casilla de Correo No. 1401, Montevideo, Uruguay 111
PITT, William, 2444 38th Avenue, Sacramento, California 95822, U.S.A. 141, 147
PODER, Mickaël, Faculté de Médecine, Brest, France 116
POIZAT, Claude, Laboratoire de Biologie marine, Faculté des Sciences et Techniques de Saint-Jérôme, 13397 Marseille Cedex 4, France 115
POLI, P., Istituto di Zoologia, Università di Parma, Parma, Italy 123
POLISHCHUK, V.V., Hydrobiological Institute, Academy of Science, Ukrainian SSR, Kiev, U.S.S.R. 127
POOL, David, Department of Biology, Stephen F. Austin State University, Nacogdoches, Texas 75962, U.S.A. 133

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POORMAN, Forrest L., Malacology Section, Los Angeles County Museum of Natural History, 900 Exposition Blvd., Los Angeles, California 90007, U.S.A. 137
POORMAN, Leroy H., Malacology Section, Los Angeles County Museum of Natural History, 900 Exposition Blvd., Los Angeles, California 90007, U.S.A. 137
POPOV, S.V., Palaeontological Institute, Academy of Sciences, Moscow, U.S.S.R. 127
PORTER, Hugh J., Institute of Marine Sciences, University of North Carolina, Morehead City, North Carolina 28557, U.S.A. 109
POZDNIAKOVA, L.A., Institute of Biology of the Sea, Academy of Sciences, Vladivostok, U.S.S.R. 127
PRASAD, R., P.G. Department of Zoology, Berhampur University, Berhampur - 7, Orissa, India 137
PRATT, William Lloyd, Museum of Natural History, University of Nevada, 4505 Maryland Parkway, Las Vegas, Nevada 89154, U.S.A. 109, 131, 147
PREZANT, Robert S., College of Marine Studies, University of Delaware, Lewes, Delaware 19958, U.S.A. 109, 134
PRICE, Richard E., Department of Biology, University of Mississippi, University, Mississippi 38677, U.S.A. 132
PRISYAZHNYUK, V.A., Institute of Geological Sciences, Academy of Science, Ukrainian SSR, Kiev, U.S.S.R. 127
PRJADKO, V.P., Hydrobiological Institute, Academy of Science, Ukrainian SSR, Kiev, U.S.S.R. 126
PUISSÉGUR, Jean-Jacques, Institut des Sciences de la Terre, Université de Dijon, L.A. no. 157, 6 Bd. Gabriel, 21100 Dijon, France 106
QADRI, S.U., Biology Department, University of Ottawa, Ottawa, Ontario, Canada 133
QUILLIEN-MONOT, Michèle, Laboratoire de Zoologie, Aquaculture et Pollutions Marines, Faculté des Sciences, 6 Avenue le Gorgeu, 29283 Brest Cedex, France 116
RADOMAN, Pavle, Faculty of Sciences, Belgrade University, Belgrade, Yugoslavia 106
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RAE, John Gibson, III, Department of Zoology and Microbiology, Ohio University, Athens, Ohio 45701, U.S.A. 140
RAFFAELLI, D.G., Department of Biology, University of Essex, Wivenhoe Park, Colchester CO4 3SQ, England 122
RAFFI, Sergio, Istituto di Geologia e Paleontologia, Università di Parma, Parma, Italy 123
RAJAGOPAL, A.S., Zoological Survey of India, 8 Lindsay Street, Calcutta 700016, India 125
RAMPAL, Jeannine, Laboratoire de Biologie Animale (Plancton), Université de Provence, Marseilles, France 123
RAO, M. Balaparameswara, Department of Zoology, Nagarjuna University, Nagarjunanagar 522510, India 121
RAUT, S.K., Zoological Survey of India, Mollusca Section, 8 Lindsay Street, Calcutta 700016, India 141
RAVERA, Oscar, Biology Group, Ispra, D.G. Research, Science and Education, C.E.C. Euratom J.R.C., 21027 Ispra, Varese, Italy 123
REAKA, Marjorie Lindquist, Department of Zoology, The University of Maryland, College Park, Maryland 20742, U.S.A. 139
REDSHAW, N.R., Department of Surgery, University of Otago Medical School, Dunedin, New Zealand 121
REEDER, Richard L., Faculty of Natural Sciences, University of Tulsa, Tulsa, Oklahoma 74104, U.S.A. 147
REISH, Donald J., Department of Biology, California State University, Long Beach, California 90840, U.S.A. 139
RÉKÁSI, József, Hősök tere 8, 6430 Bácsalmás, Hungary 135
REZNICHENKO, O.G., Institute of Oceanology, Academy of Sciences, Moscow, U.S.S.R. 126
RHOADS, Donald C., Department of Geology and Geophysics, Yale University, New Haven, Connecticut 06520, U.S.A. 109
RICHARD, Alain, Université de Lille I, Laboratoire de Biologie et Ecologie Marines, SN3, B.P. 36, 59650 Villeneuve-d'Ascq, France 115
RICHARD, Georges, Laboratoire de Biologie Marine et de Malacologie, Ecole Pratique Hautes Etudes - Museum, 55 rue Buffon, 75005 Paris, France 116
RICHARDOT, Monique, Laboratoire de Biologie animale et Ecologie, Université Claude-Bernard - Lyon I, 43, Bd du 11 Novembre 1918, 69621 Villeurbanne, France 125

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RICHARDS, Charles S., Laboratory of Parasitic Diseases, National Institute of Allergy and Infectious Diseases, National Institutes of Health, Bethesda, Maryland 20014, U.S.A. 124
RICHARDS, Horace G., Academy of Natural Sciences, 19th and the Parkway, Philadelphia, Pennsylvania 19103, U.S.A. 132
RICHNOVSZKY, Andor, Dózsa György u. 12-14, 6500 Baja, Hungary 135
RINALDI, Emidio, Via Marengo 29, Forlì, Italia 113
RIOS, E.C., Sección de Malacología, Museo Oceanográfico de Rio Grande, Río Grande do Sul, Brasil 109
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RIVA, Alain, Laboratoire de Biologie marine, Faculté des Sciences et Techniques de Saint-Jérôme, 13013 Marseille Cedex 4, France 115
ROBERTS, H. Wallace, Krusen Evans and Byrne, Philadelphia, Pennsylvania, U.S.A. 109
ROBERTS, Tyson R., Tiburon Center for Environmental Studies, San Francisco State University, P.O. Box 855, Tiburon, California 94920, U.S.A. 109
ROBERTSON, J. Roy, Marine Institute, University of Georgia, Sapelo Island, Georgia 31327, U.S.A. 133
RODDA, Peter U., Department of Geology, California Academy of Sciences, San Francisco, California 94118, U.S.A. 117
ROGERS, Steffen H., Faculty of Natural Sciences, University of Tulsa, Tulsa, Oklahoma 74104, U.S.A. 147
ROGINSKAYA, I.S., Institute of Oceanology, Academy of Sciences, Moscow, U.S.S.R. 126
ROGUES, Olivier, Tioxide S.A., B.P. 89, 62102 Calais, France 115
ROMANENKO, V.D., Hydrobiological Institute, Academy of Science, Ukrainian SSR, Kiev, U.S.S.R. 126
ROMERO, Faustino RODRIGUEZ-, Universidad Nacional Autónoma de México, Centro de Ciencias del Mar y Limnologia, México 20, D.F., Mexico 145
ROSEN, Marc David, Department of Biology, Sonoma State College, Rohnert Park, California 94928, U.S.A. 138
ROSEWATER, Joseph, Department of Invertebrate Zoology, Division of Mollusks, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, U.S.A. 109, 132
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ROTH, Barry, Department of Geology, California Academy of Sciences, San Francisco, California 94118, U.S.A. 147
RUBIO, Efrain A., Departamento de Biologia, Universidad del Valle, A.A. 2188, Cali, Colombia 147
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RUNHAM, N.W., Department of Zoology, University College of North Wales, Bangor, Gwynedd, U.K. 124
RUSSELL, Henry D., Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138, U.S.A. 133
SABELLI, Bruno A., Istituto di Zoologia dell'Università di Bologna, Bologna, Italy 112, 113, 114
SACCHI, Cesare F., Istituto di Ecologia Animale ed Etologia, Università di Pavia, 27100 Pavia, Italy 123
SAKURAI, Kin'ichi, National Science Museum, Natural History Institute, Ueno Park, Tokyo 160, Japan 142
SATHANANTHAN, A. Henry, Department of Biological Sciences, Lincoln Institute, 625 Swanston Street, Carlton, Victoria 3053, Australia 119
SCANLAND, Thomas B. [no address given] 141
SCARLATO, O.A., Zoological Institute, Academy of Sciences of the U.S.S.R., Leningrad B-164, U.S.S.R. 125
SCHELTEMA, Amelie H., Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543, U.S.A. 124
SCHIEBE, Frank R., U.S. Sedimentation Laboratory, Agricultural Research Service, Oxford, Mississippi 38655, U.S.A. 132
SCHIKOW, E.W., Zoologisches Institute, Akademie der Wissenschaften der U.S.S.R., Leningrad, U.S.S.R. 106
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SCHMEKEL, Luise, Zoologisches Institute der Westfälischen Wilhelms-Universität, Hüfferstrasse 1, D-4400 Münster (Westf.), Germany (FR) 140
SCHÜTT, Hartwig, Haydnstrasse 50, D-4 Düsseldorf-Benrath, Germany (FR) 106
SEAGER, J.R., British Antarctic Survey, Madingley Road, Cambridge CB3 0ET, England 122
SEILKOP, Steven K., Department of Zoology and Academic Computer Service, Miami University, Oxford, Ohio 45056, U.S.A. 109
SELANDER, Robert K., Center for Evolution and Paleobiology, University of Rochester, Rochester, New York 14627, U.S.A. 137
SHANNON, Allan, Veterans Administration Hospital, 4500 South Lancaster Road, Dallas, Texas 75216, U.S.A. 147
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SHEJGUS, V.E., Institute of Biology of the Sea, Academy of Sciences, Vladivostok, U.S.S.R. 127
SHILEYKO, A.A., Benthos Laboratory, Institute of Oceanology, Academy of Sciences of the U.S.S.R., Krassikova ul. 23, Moscow 117218, U.S.S.R. 124
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SHMAKOV, V.T., Pedagogical Institute, Smolensk, U.S.S.R. 126
SHONMAN, David, Moss Landing Marine Laboratories, P.O. Box 223, Moss Landing, California 95039, U.S.A. 138
SICARDI, Omar E., Coquimbo 2371, Montevideo, Uruguay 111
SIDDALL, Scott E., School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, Florida 33149, U.S.A. 109
SIEBERT, A.E., Jr., Department of Zoology, University of California, Berkeley, California 94720, U.S.A. 138
SIGURDSSON, J.B., Dove Marine Laboratory, Cullercoats, Tyne and Wear NE30 4PZ, England 121
SILBERZAHN, Nadine, Groupe d'Endocrinologie Comparée, Laboratoire de Zoologie, Université de Caen, Esplanade de la Paix, 14032 Caen Cedex, France 116
SILINA, A.V., Institute of Biology of the Sea, Academy of Sciences, Vladivostok, U.S.S.R. 127
SIMPSON, J.F., School of Biology, University College, P.M.B. 5323, Port Harcourt, Nigeria 121
SIRENKO, B.I., Zoological Institute, Academy of Sciences of the U.S.S.R., Leningrad B-164, U.S.S.R. 125
SLAVOSHEVSKAYA, L.V., Zoological Institute, Academy of Sciences of the U.S.S.R., Leningrad B-164, U.S.S.R. 126
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SMIGIELSKI, Francis, Institut de Biologie Maritime et Régionale, Avenue Foch, 62930 Wimereux, France 115
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SMITH, Brian J., National Museum of Victoria, Melbourne, Victoria, Australia 119
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SOLEM, Alan, Department of Zoology, Field Museum of Natural History, Roosevelt Road at Lake Shore Drive, Chicago, Illinois 60605, U.S.A. 109, 147
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SOLOMATINA, V.D., Hydrobiological Institute, Academy of Science, Ukrainian SSR, Kiev, U.S.S.R. 126
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SORBI, Enrico, Via delle Ginestre 43/18, Genova, Italy 113
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SOUPLET, Arnaud, Institut de Biologie Maritime et Régionale, Avenue Foch, 62930 Wimereux, France 115
SPADA, Gianni, Via San Felice 26, 40122 Bologna, Italy 112, 113, 114

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SPHON, Gale G., Department of Invertebrate Zoology, Los Angeles County Museum of Natural History, 900 Exposition Blvd., Los Angeles, California 90007, U.S.A. 139
SPICHAK, S.K., Azov Research Institute of Fishery, Kerch, U.S.S.R. 126
SPIGHT, Tom M., Woodward-Clyde Consultants, 3 Embarcadero Center, Suite 700, San Francisco, California 94111, U.S.A. 138
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STAROBOGATOV, Ya. I., Zoological Institute, Academy of Sciences of the U.S.S.R., Leningrad B-164, U.S.S.R. 125
STASEK, Charles R., Department of Biology, Sonoma State College, Rohnert Park, California 94928, U.S.A. 138
STRENTH, Ned E., Marine Biomedical Institute, University of Texas Medical Branch, Galveston, Texas 77550, U.S.A. 138
STUMPF, Jerry, Department of Ecology and Behavioral Biology, University of Minnesota, Minneapolis, Minnesota 55455, U.S.A. 122
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TABUNKOV, V.D., Sakhalin Department of the Pacific Research Institute of Fishery and Oceanography, Antonovo, U.S.S.R. 126
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TANG CHRISTENSEN, J., Department of Ecology and Genetics, Ny Munkegade, University of Arhus, 8000 Arhus C, Denmark 120
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TARDY, Jean, Laboratoire de Biologie, Biochimie Marines et Phycoécologie, Université de Poitiers, IUT de La Rochelle, 17026 La Rochelle, France 115, 116
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TESTUD, Anne-Marie, Muséum National d'Histoire Naturelle, Laboratoire de Biologie des Invertébrés Marins et Malacologie, 55 rue de Buffon, 75005 Paris, France 116
THOMAS, W. Stephen, Rochester Museum and Science Center, Rochester, New York 14610, U.S.A. 133
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THORARINSSON, G., Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia V5A 1S6, Canada 139
TILLIER, Simon, Laboratoire de Biologie des Invertébrés Marins et de Malacologie, Muséum National d'Histoire Naturelle, 55 rue de Buffon, 75005 Paris, France 137, 140

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TIMM, V. J., Institute of Zoology and Botany, Academy of Sciences of the Estonian SSR, Tartu, U.S.S.R. 126
TOBACH, Ethel, Department of Animal Behavior, The American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024, U.S.A. 137
TODD, Christopher D., Department of Marine Biology, Marine Science Laboratories, Menai Bridge, Anglesey, Gwynedd LL59 5EH, Wales 121, 122
TOLSTIKOVA, N.V., Institute of Limnology, Academy of Sciences, Leningrad, U.S.S.R. 127
TORELLI, Alberto R., Istituto di Ecologia Animale ed Etologia, Università di Pavia, Pavia, Italia 123
TORTORICI, Rosalba, Istituto Sperimentale Talassografico, via Roma 3, 74100 Taranto, Italia 123
TRANCART, Marc, Station marine d'Endoume, 7 rue de la Batterie-des-Lions, 13007 Marseille, France 116
TSUCHI, Ryuichi, Geoscience Institute, Faculty of Science, Shizuoka University, Shuzuoka 422, Japan 139
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TSUKADA, Osamu, Toba Aquarium, Toba, Mie Prefecture 517, Japan 146
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TULLOCH, L., Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia V5A 1S6, Canada 139
TUNG, Ih-Hsiu, Institute of Fishery Biology, National Taiwan University, Taipei, Taiwan, Republic of China 110, 138
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UVALIEVA, K.K., Institute of Zoology, Academy of Science, Kazakh SSR, Alma-Ata, U.S.S.R. 125
VAGVOLGYI, Joséph, Biology Department, College of Staten Island, Staten Island, New York 10301, U.S.A. 109
VAIL, Virginia A., Tall Timbers Research Station, Route 1, Box 160, Tallahassee, Florida 32303, U.S.A. 109, 124, 125
VAN DEVENDER, Amy Shrader, Museum of Zoology, The University of Michigan, Ann Arbor, Michigan 48109, U.S.A. 125, 134
VAN ZANDT, Dirk, Research Tower, Analytical Department, Microscopy, Ethicon, Inc., Somerville, New Jersey 08876, U.S.A. 124
VARAKSIN, A.A., Institute of Biology of the Sea, Academy of Sciences, Vladivostok, U.S.S.R. 126
VARGA, András, Mátra Múzeum, Kossuth u. 40, 3200 Gyöngyös, Hungary 135
VATER, Gisela, Staatliches Museum für Naturkunde - Forschungsstelle - Görlitz, Am Museum 1, DDR-89 Görlitz, Germany (DR) 129
VEGAS VELEZ, Manuel, Ciencias del Mar, Oficina Regional de Ciencia y Tecnología de la UNESCO para América Latina y el Caribe, Casilla 859, Montevideo, Uruguay 111
VEIL, John A., Department of Zoology, University of Maryland, College Park, Maryland 20742, U.S.A. 124
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VERDCOURT, Bernard, Spring Cottage, Kimbers Lane, Maidenhead, Berkshire, England 108
VERDUIN, A., Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands 108
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VESSELSKI, S.P., Hydrobiological Institute, Academy of Science, Ukrainian SSR, Kiev, U.S.S.R. 126
VICENTE, Nardo, Laboratoire de Biologie Marine, Faculté des Sciences et Techniques, Centre de Saint-Jérôme, 13397 Marseille Cedex 2, France 115, 116

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WELLS, Fred E., Western Australian Museum, Perth, Western Australia, Australia 6000 119, 121
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WEST, David L., Biology Program, Sangamon State University, Springfield, Illinois 62708, U.S.A. 138, 141
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WHITNEY, R.A., 2140 North Main Street, Decatur, Illinois 62526, U.S.A. 140
WICKSTEN, Mary K., Allan Hancock Foundation, University of Southern California, University Park, Los Angeles, California 90007, U.S.A. 138
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WRIGHT, William G., Moss Landing Marine Laboratories, Moss Landing, California 95039, U.S.A. 147
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ZORINA, I.P., Zoological Institute, Academy of Sciences of the U.S.S.R., Leningrad B-164, U.S.S.R. 126
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VOLUMES, ISSUES AND PUBLICATION DATES OF *MALACOLOGICAL REVIEW*. – *Malacological Review* was first published in one number for the year 1968. This single issue (187 pages) constituted Volume 1. For each of the years from 1969 to 1974 (Vols, 2, 3, 4, 5, 6 and 7), two semiannual numbers were published, each two issues for a calendar year constituting a volume. Beginning with Vol. 4 (1971), each of the two annual issues were formally designated as a "number", the first issue of each volume being "Vol. _, No. 1" and the second issue "Vol. _, No. 2". In 1975 (Vol. 8), 1976 (Vol. 9), 1977 (Vol. 10) and 1978 (Vol. 11), both issues for each calendar year were combined and designated as "Vol. _, No. 1-2". Each volume normally consists of about 200 pages.

Publication dates of past issues are as follows: Vol. 1, 7 June 1969; Vol. 2 [No. 1], pages 1-102, 10 June 1969; Vol. 2 [No. 2], pages 103-214, 8 May 1970; Vol. 3 [No. 1], pages 1-102, 28 May 1970; Vol. 3 [No. 2], pages 103-192, 13 March 1971; Vol. 4, No. 1, 27 July 1971; Vol. 4, No. 2, 10 February 1972; Vol. 5, No. 1, 31 July 1972; Vol. 5, No. 2, 12 January 1973; Vol. 6, No. 1, 12 April 1973; Suppl. 1, 25 October 1973; Vol. 6, No. 2, 29 January 1974; Vol. 7, No. 1, 3 July 1974; Vol. 7, No. 2, 30 September 1974; Vol. 8, No. 1-2, 15 May 1975; Vol. 9, No. 1-2, 26 March 1976; Vol. 10, No. 1-2, 3 March 1978; Vol. 11, No. 1-2, 20 July 1978.

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